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Population Ecology of the Beach Mouse, Peromyscus Polionotus Niveiventris

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POPULATION ECOLOGY OF THE BEACH MOUSE, *PEROMYSCUS POLIONOTUS NIVEIVENTRIS*

BY

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THESIS

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INTRODUCTION

The cricetid rodent Peromyscus polionotus is limited to the southeastern United States, where two ecological forms are recognized: old field mice and beach mice. Old field mice occupy dry sandy habitats on inland sites in Alabama, Georgia, South Carolina, and Florida (Schwartz, 1954; Blair et al., 1968). Beach mice occur on the coastal dunes on the west and east coasts of Florida (Ivey, 1949; Blair, 1951). The old field form is relatively well studied in terms of population ecology (Caldwell, 1964; Davenport, 1964; Golley et al., 1965; Smith, 1967a, 1968a, 1971; Briese and Smith, 1974), behavior (Smith, 1967b; Smith and Criss, 1967; Dewsbury, 1971; Kaufman et al., 1974; O'Farrell and Kaufman, 1975; Garten, 1976), and genetics (Biggers and Dawson, 1971; Selander et al., 1971; Te and Dawson, 1971). In contrast, relatively few studies have been reported on the beach forms. Blair's (1951) study of P. p. leucocephalus, a subspecies found on the Gulf Coast of Florida, represents the only known population analysis. More recently Bowen (1968) has discussed the evolution of the Gulf coast forms. Selander et al. (1971) discussed genic heterozygosity in several populations of beach mice from the east and west coasts of Florida. Ehrhart (1971) investigated the behavior of three subspecies from the west coast of Florida. Dapson (1972) presented demographic data with emphasis on age structure of a population of P. p. niveiventris sampled at Vero Beach, Florida.

This study of P. p. niveiventris covered a period of 37 months, 1976-1979, at two sites on the east coast of Florida, selected to represent optimal and marginal habitats. The overall purpose of the study was to document community dynamics of rodents and vegetation at the coastal sites. Keim (1979) and Stout (1979) have discussed the general results. This paper is concerned with demographic adjustments of P. p. niveiventris during a period of unusual population increase at the optimal site in 1978-79; contrasts with the population in marginal habitat are made. Companion papers will deal with (1) dispersion and movements, and (2) long-term population dynamics of the species.

Free ranging populations of Peromyscus seldom attain high densities or undergo the fluctuations in numbers charateristic of many microtines (Terman, 1968; Krebs and Myers, 1974). Self regulation of population size has been suggested by many researchers. One hypothesis is that aggression of adult males during the breeding season suppresses the survival of immature animals (Sadleir, 1965; Healey, 1967; Petticrew and Sadleir, 1974; Fairbairn, 1977). Another hypothesis is that resident females regulate the population by excluding immigrant females from their home ranges (Nicholson, 1941; Metzgar, 1971).

These hypotheses were derived from studies conducted in temperate areas where Peromyscus sp. have distinct breeding seasons. In peninsular Florida, which has a subtropical climate, reproductive activity of Peromyscus sp., e.g., P. gossypinus and P. polinotus, is usually centered in late summer, fall, and early winter months, but can occur

during all months. Recently accumulated evidence (Bigler and Jenkins, 1975; Smith and Vrieze, 1979; Stout, 1979) suggests that in peninsular Florida these species may achieve greater densities and undergo more striking fluctuations in abundance than is typical of temperate regions. These differences may be accounted for by variations in reproductive success between and among years in a more benign climatic setting. Therefore, regulation of populations in areas with poorly delimited breeding seasons may be fundamentally different from the patterns described from more temperate environments.

MATERIALS AND METHODS

Description of Study Areas

The two trapping grids were located on the north end of the Canaveral Peninsula portion of Merritt Island, Brevard Co., Florida, USA (Fig. 1). The "beach grid" was immediately adjacent to the high tide mark and extended inland from the ocean over two minor dune lines, a major dune (6 m above sea level) and 30 m beyond the crest of the major dune line. Three obvious zones of vegetation ran parallel with the beach and dune lines. Zone 1 was the most seaward and was covered primarily with sea oats Uniola paniculata, sunflower Heterotheca subaxillaris, and morning glories Ipomoea stolonifera and I. pes-caprae. Zone 1 varied in width from 40-50 m. Zone 2 was located between zone 1 and the major dune line. Much of this zone was bare sand with clumps of palmetto Serenoa repens, a few sea grape Coccoloba uvifera, and buckthorn Bumelia tenax. Gopher apple Licania michauxii formed extensive mats in some places. Zone 2 was approximately 45 m in width. Zone 3 began at the top of the major dune line and extended inland several hundred meters. It consisted of a dense shrub layer. Palmetto and sea grape were most abundant while wax myrtle Myrica cerifera, buckthorn and snowberry Chiococca alba were common but scattered. There was almost no ground cover beneath the shrubs, but a heavy litter was present. Small areas of bare sand were present. The grid extended about 30 m into zone 3.

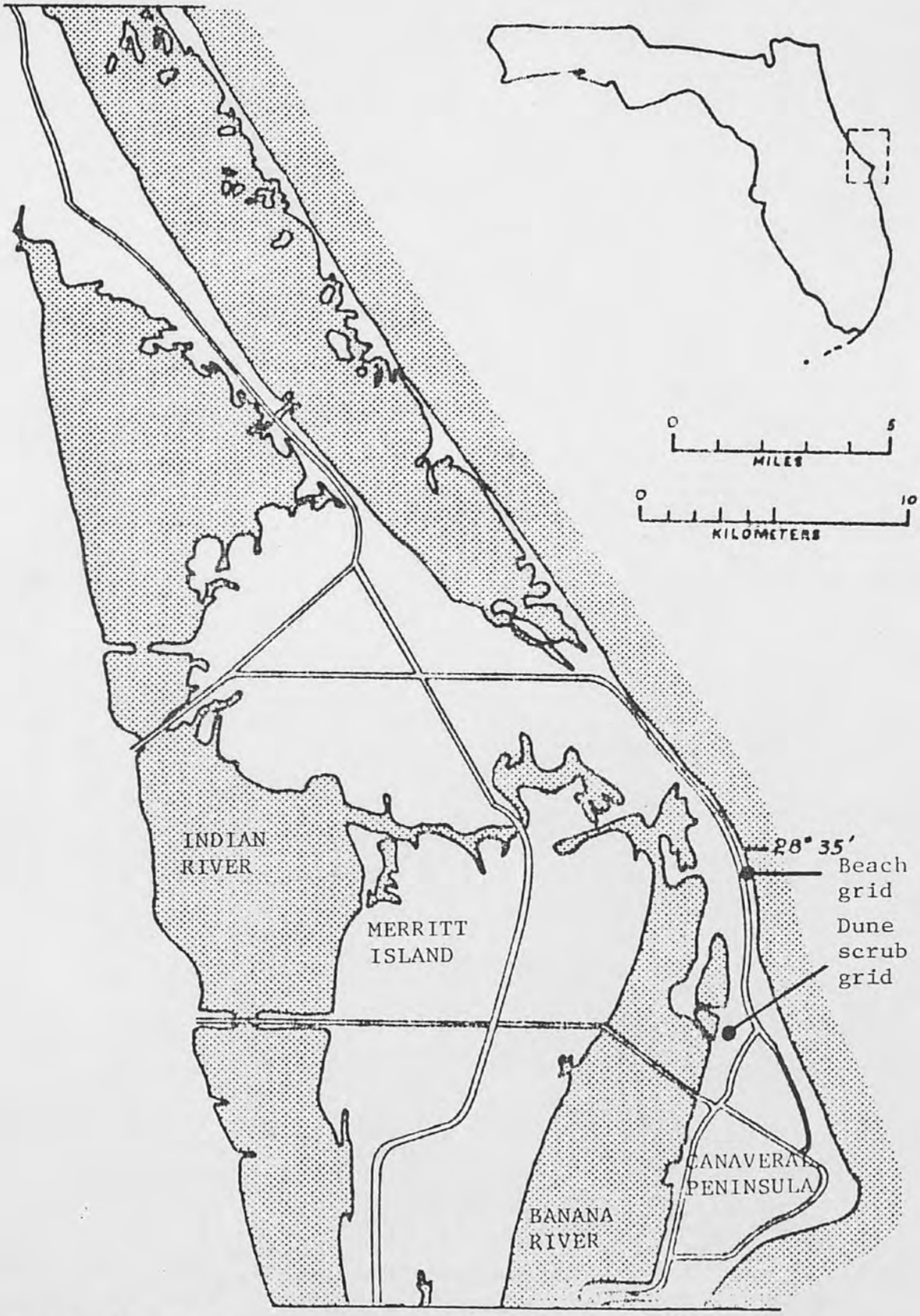

Fig. 1. Locations of the beach and dune scrub grids on the Canaveral Peninsula portion of Merritt Island, Brevard Co., USA.

The "dune scrub grid" was on an old dune area about 1 km from the beach (Fig. 1). The relief was level. A dense shrub cover 1-2 m in height covered the grid. The grid was surrounded by extensive acreage of similar vegetation. Essentially no ground level cover was present, but a heavy litter was present beneath the shrubs. Rosemary Ceratiola ericoides formed extensive, almost pure stands in some places. Live oak Quercus virginiana var. maritima, chapman oak Q. chapmani, and myrtle oak Q. myrtifolia were common. Spanish plum Ximenia americana, rusty lyonia Lyonia ferruginea, and palmetto were scattered throughout the grid.

Trapping Procedures

Trap stations were arranged in an 8 x 8 pattern (1.44 ha) with 64 traps positioned 15 m apart. Both grids were set up in 1975 and, prior to the present study, had been trapped monthly since July 1976 (Keim, 1979; Stout, 1979). Single Sherman live traps (8 x 9 x 23 cm) were placed within 1-2 m of each trap station. When overall trap success exceeded 50%, based on the original 64 traps, 56 extra traps were added, to ensure a surplus of traps (Krebs et al., 1976). Extra traps were placed on the columns half-way between the trap stations. All traps were opened during the afternoon, baited with oak flakes, and checked for captures the next morning. The dune scrub grid was trapped at monthly intervals from June 1978 to July 1979. The beach grid was trapped at monthly intervals from June 1978 to September 1978 and at approximate two week intervals from October 1978 to July 1979.

P. polionotus were marked with numbered monel ear tags, sexed, classified as juvenile, subadult, or adult by pelage characteristics and weighed with a Pesola spring balance. Reproductive status of males was determined by position of the testes: abdominal, partially-descended, or descended. Female reproductive status was determined by the condition of the vagina (perforate or imperforate), mammaries (small or enlarged), and the symphasis pubis (closed or notched). Mice were released at the point of capture.

Population counts were based on the minimum number known to be alive (Krebs, 1966). Survival rates were calculated as the inverse ratio of the number of animals known to be alive during trap period (t) to the number of those animals that were known to be alive the next time period (t + 1). Overall trappability was defined as the ratio of the number of residents captured in a trap period to the number of residents that were known to be alive during that trap period, whereas individual trappability (Hilborn et al., 1976) was defined as the ratio of the number of trap periods an individual was captured, first and last captures excluded, to the total number of trap periods between that individuals first and last capture.

RESULTS

Capture Success and Trappability

In 2256 trap nights on the beach grid from June 1978 to July 1979 a total of 227 individual P. polionotus were captured 771 times for a capture success of 0.34. During the same time period 896 total trap nights on the dune scrub grid yielded 99 captures of 58 individual beach mice for a capture success of 0.11. The greater capture success of the beach grid is further amplified because 56 traps were added to the grid from January to July 1979. Average overall trappability of beach mice was 61% on the beach grid and 53% on the dune scrub grid.

Minimum Numbers and Densities

Minimum numbers of Peromyscus polionotus on the beach grid dropped from 23 in July 1978 to a low of 16 in October 1978 (Fig. 2). After October the minimum numbers increased exponentially to a high of 97 animals (67/ha) in March 1979. The instantaneous rate of population growth (r) (Caughley and Birch, 1971) per week during this time period was 0.092. This represents a doubling time of approximately 7.9 weeks. Minimum numbers remained stable from March until mid-April when they started to decline and continued to decline throughout the duration of the study ($r = -0.059$.)

During the summer and fall months of 1978 beach mice maintained stable densities (Table 1). Densities increased during the winter

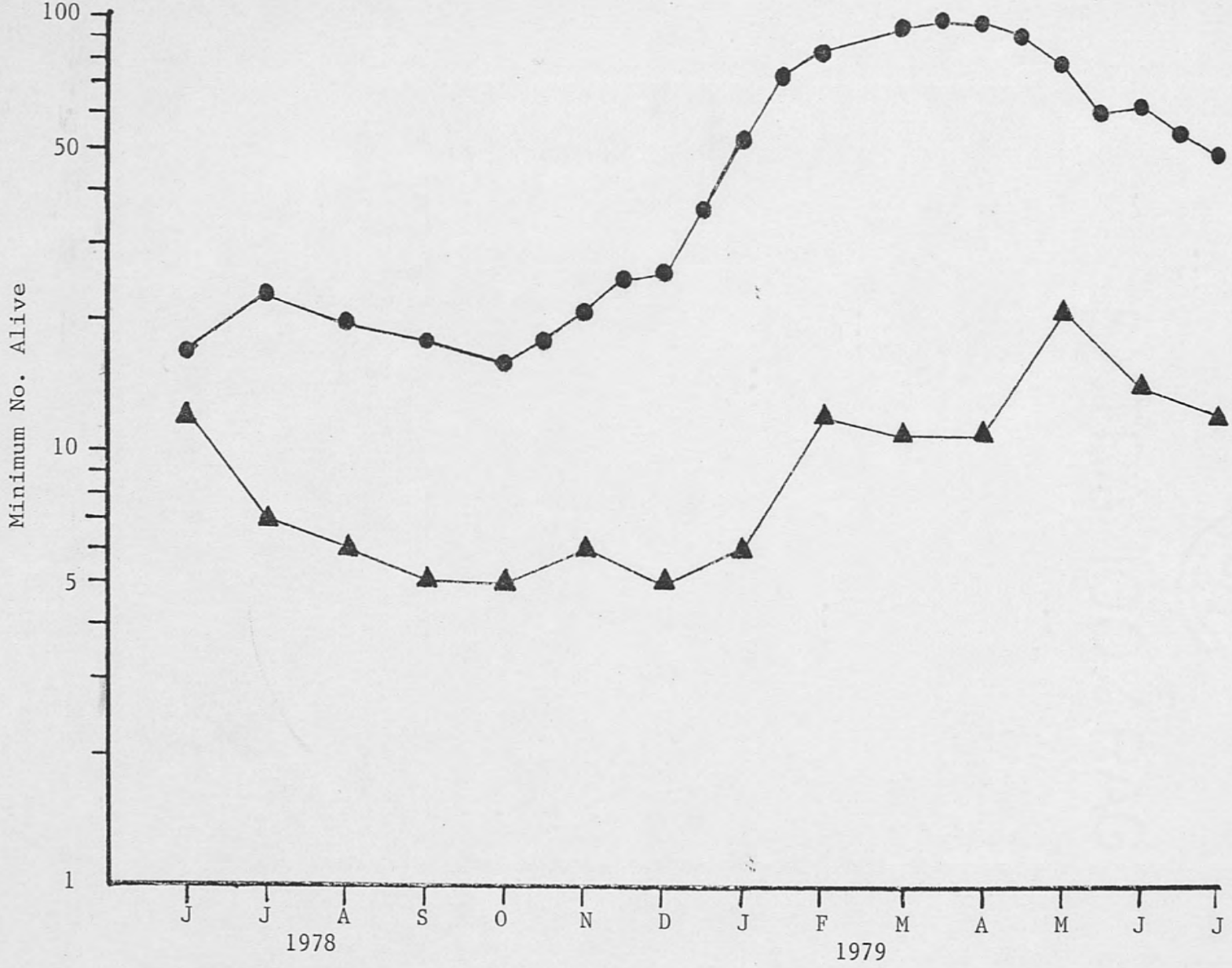

Fig. 2. Minimum numbers alive on the beach grid (●) and dune scrub grid (▲).

Table 1. Seasonal densities on the beach and dune scrub grids. Standard error in parentheses. Densities presented are the averages of the minimum numbers for the trap periods and the effective area of capture is assumed to be 1.44 ha.

Season	Year	No./ha			
		Beach grid		Dune scrub grid	
		$\bar{x}$	(SE)	$\bar{x}$	(SE)
Summer	1978	13.9	(1.20)	5.8	(1.28)
Fall	1978	13.6	(1.08)	3.7	(0.23)
Winter	1978	37.2	(7.28)	5.3	(1.51)
Spring	1979	59.7	(4.09)	10.0	(2.31)
Summer[a]	1979	38.0	(2.81)	9.0	(0.69)

a Includes only June and July

($\bar{x}$ = 37.2/ha) and peaked in the spring ($\bar{x}$ = 59.7/ha). The density was at least 50/ha for almost three months, February 15 through May 5, and remained significantly higher during the summer of 1979 ($\bar{x}$ = 38.0/ha) than the summer of 1978 ($\bar{x}$ = 13.9/ha) ($t = 10.38$; $p < 0.001$).

The cumulative number of individual mice encountered through time on the beach grid (Fig. 3) shows that there was recruitment throughout the course of the study. Recruitment during the increase phase was quite high ($\bar{x}$ = 0.91 ind./day) but was still present during the decrease phase ($\bar{x}$ = 0.48 ind./day).

The minimum number of beach mice on the dune scrub grid was lower than on the beach grid during all trap periods of the study (Fig. 2). As on the beach grid minimum numbers decreased from the summer (12) to a low (5) in the fall. Unlike the beach grid the minimum numbers remained fairly stable from September 1978 to January 1979. Minimum number increased in February (12), remained fairly stable through April and then increased to a peak of 21 animals (14.6/ha) in May. Thus the peak in minimum number on the dune scrub (21) was much lower than on the beach grid (97) and occurred almost two months later.

Seasonal densities were much lower on the dune scrub than on the beach grid (Table 1). The most striking differences were in the winter, spring and summer seasons. On the dune scrub grid the density during the summer of 1978 ($\bar{x}$ = 5.8/ha) was not much different than during the summer of 1979 ($\bar{x}$ = 9.0/ha). This contrasts with the almost threefold increase in density on the beach grid between the summer of 1978 and 1979.

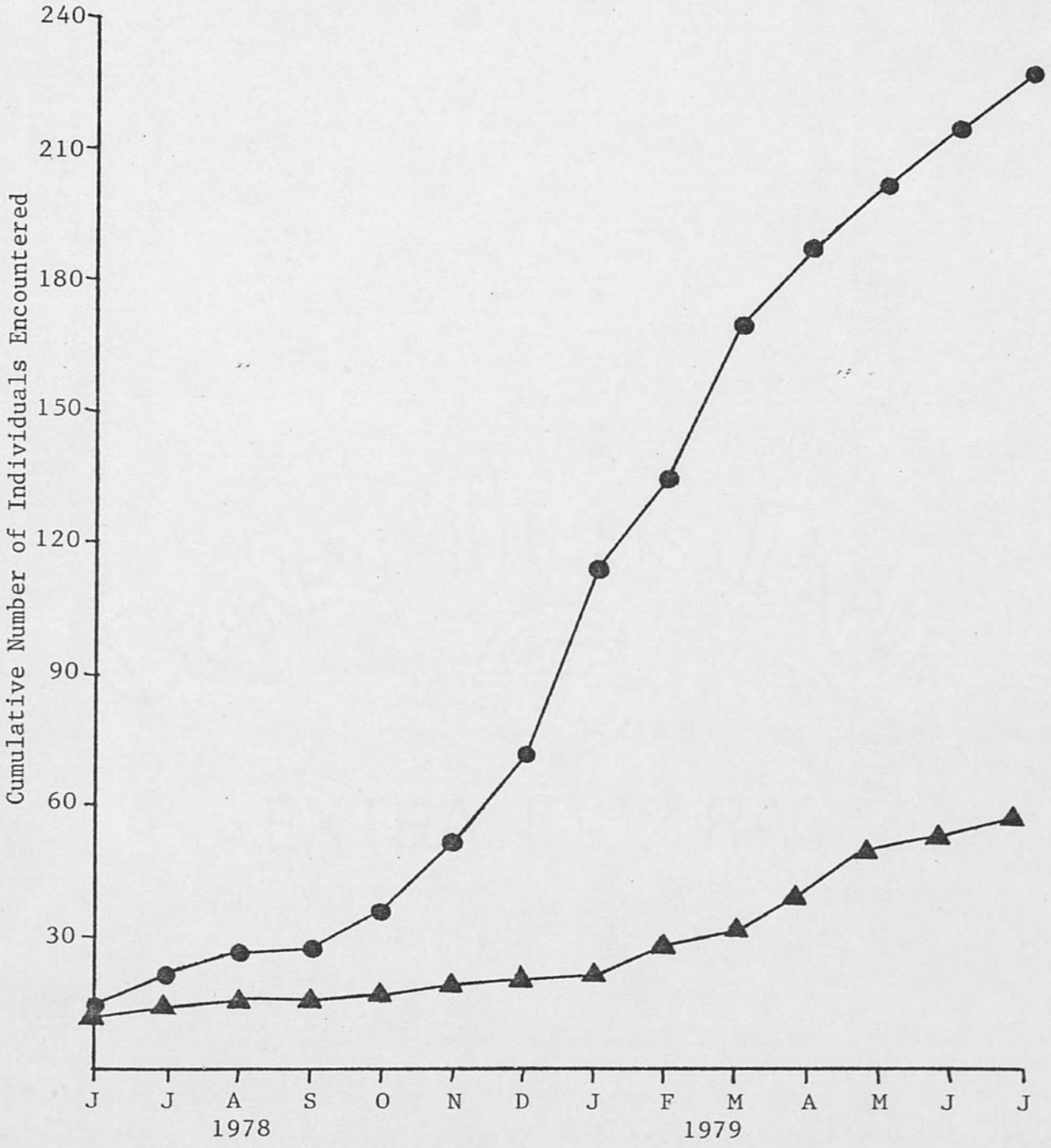

Fig. 3. Cumulative number of individuals encountered on the beach grid (●) and the dune scrub grid (▲).

The cumulative number of individuals encountered through time on the dune scrub (58) was much lower than on the beach grid (227) (Fig. 3). Recruitment was fairly low in both habitats from June until October 1978 and remained low on the dune scrub until February 1979. The recruitment rate of beach mice on the dune scrub grid during the population increase ($\bar{x}$ = 0.23 ind./day) was lower than during the population decrease on the beach grid ($\bar{x}$ = 0.48 ind./day).

Survival and Residency Time

Survival rates of male and female beach mice on the beach grid were similar within trap periods, except for slightly higher survival of males during the fall months (Fig. 4). Survival of both sexes increased in December 1978 and remained quite high until late April 1979.

Survivorship curves for monthly trap cohorts on the beach grid (Fig. 5) revealed that survivorship curves for October and November trap cohorts showed a sharp initial drop, due to low survival of new animals, and then a leveling off as survival of resident animals was higher. In fact, the animals recruited in October and November that became residents survived very well from November-December until April. Starting with the December trap cohort the sharp initial drop in the survivorship curves is missing and only a slight decrease in numbers through time is apparent. This trend continued until the early spring trap cohorts (April-May), which showed a return to lower survival of new animals. Trap cohorts from December-February were only reduced approximately 50% by April. This was particularly significant because a large number of the individuals from these trap cohorts became re-

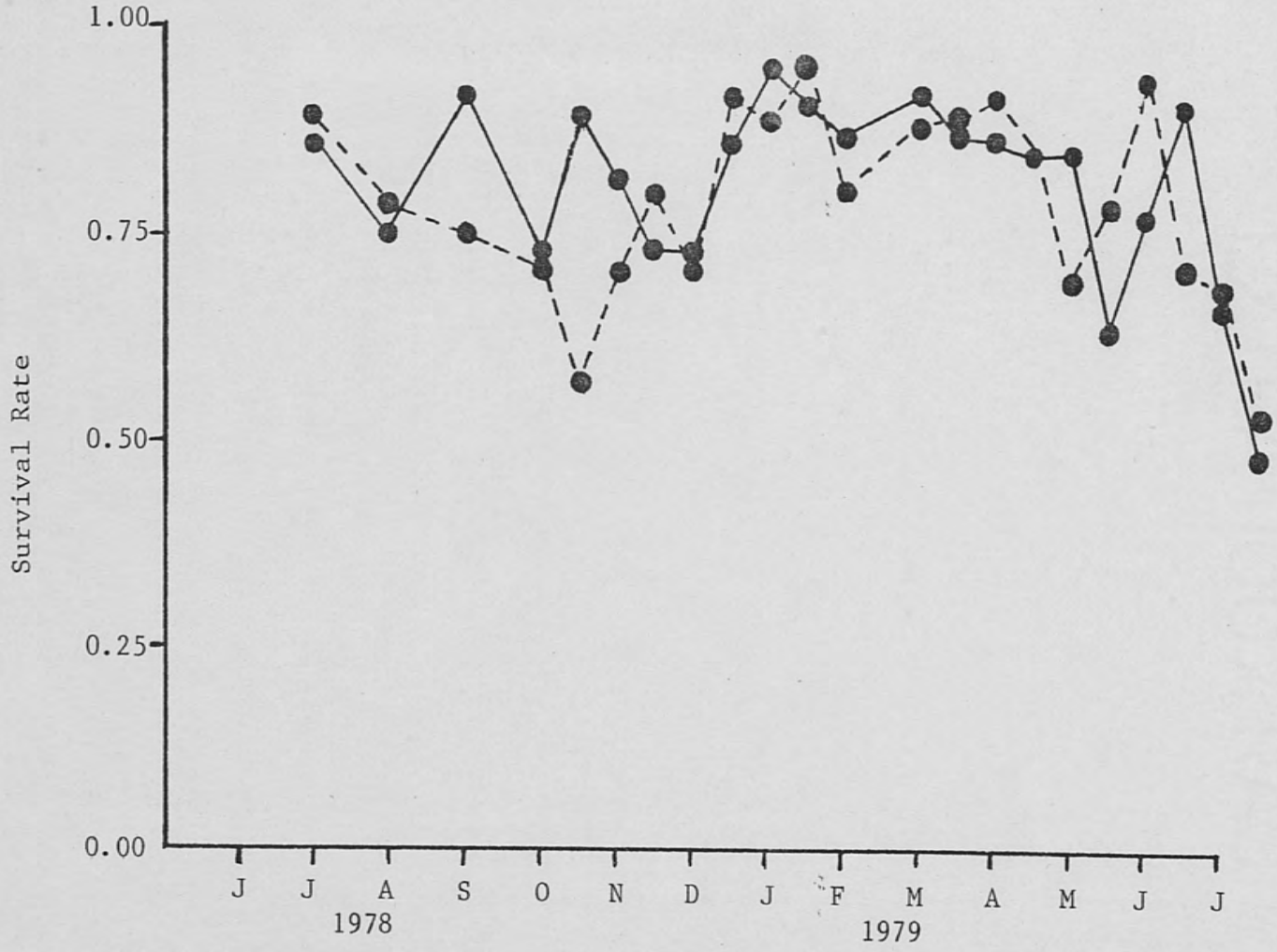

Fig. 4. Survival rates of males (solid lines) and females (dotted lines) on the beach grid.

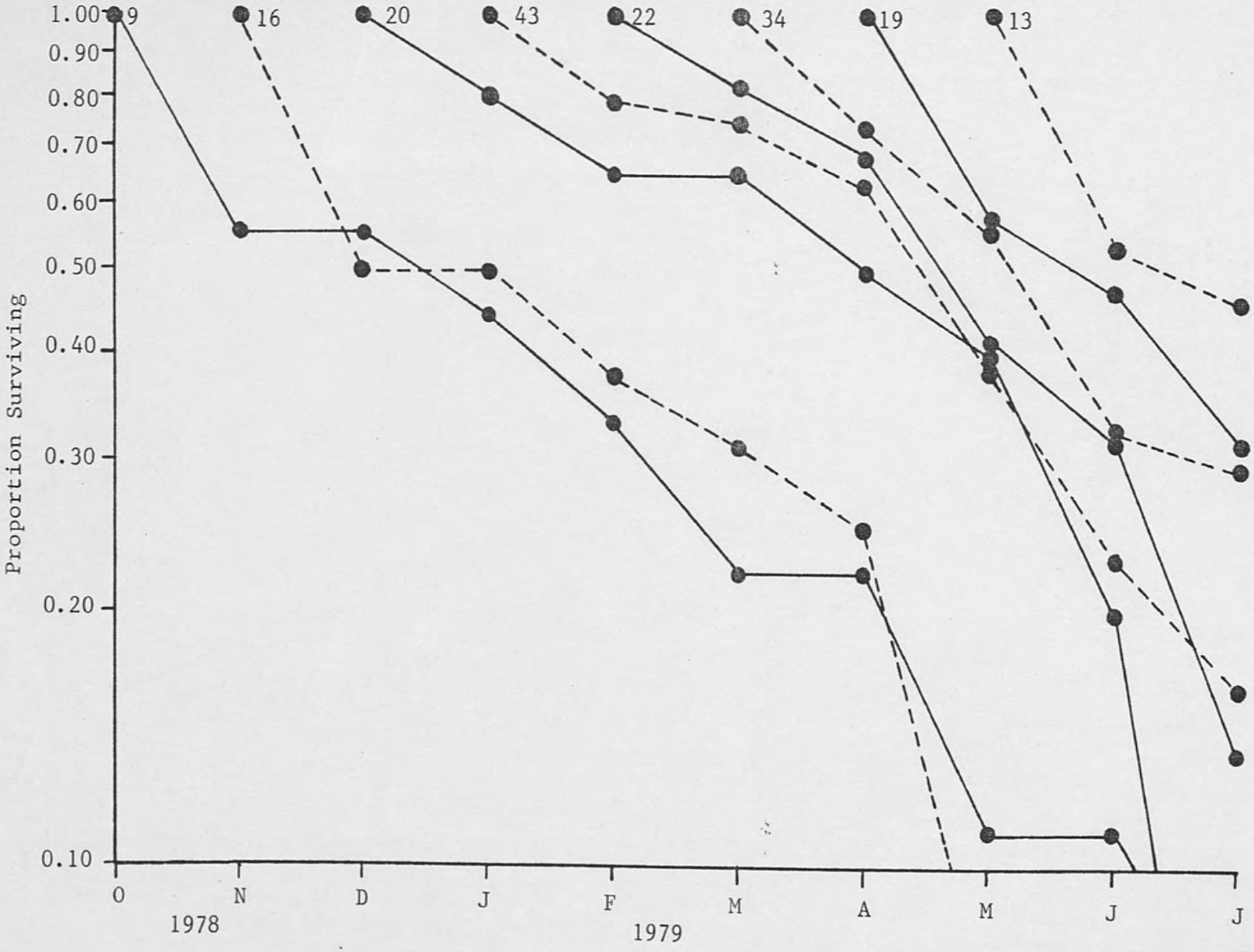

Fig. 5. Monthly trap cohort survivorship curves for beach mice on the beach grid. Sample sizes are given at the top.

productively active.

The average length of residency of all beach mice on the beach grid was 12.4 weeks. Fifty-nine (26%) of the 221 beach mice were only captured once. Average residency of mice captured more than once was 15.6 weeks. The frequency distribution of residency times (Fig. 6) is nearly even from week 4 to 22, an indication of excellent recapture survival.

Survival of beach mice on the dune scrub grid ($\bar{x}$ = 69.8%) (Fig. 7) was not as high as on the beach grid ($\bar{x}$ = 81.0%) (Fig. 4). Due to smaller sample sizes separate rates were not calculated for male and female mice, or monthly cohorts. Survival was low on the dune scrub during summer 1978 ($\bar{x}$ = 57%), when the minimum numbers dropped from 12 animals in June to 5 in September and October. During the fall survival increased ($\bar{x}$ = 86%) but then decreased slightly during the winter months ($\bar{x}$ = 77%). Survival was low in March and April 1979 (50% and 54%, respectively), but increased in May (91%), the month with the highest minimum number (21). New animals did not survive as well as resident animals. The periods of highest survival of beach mice on the dune scrub were when few new animals were being recruited into the population. The trap periods in which animals exhibited lower survival were when new animals were appearing on the grid in greater numbers.

Twenty-six (44%) of the 58 beach mice captured on the dune scrub were only captured once. This was a higher percentage of single captures than on the beach grid (26%). Average residency time of all

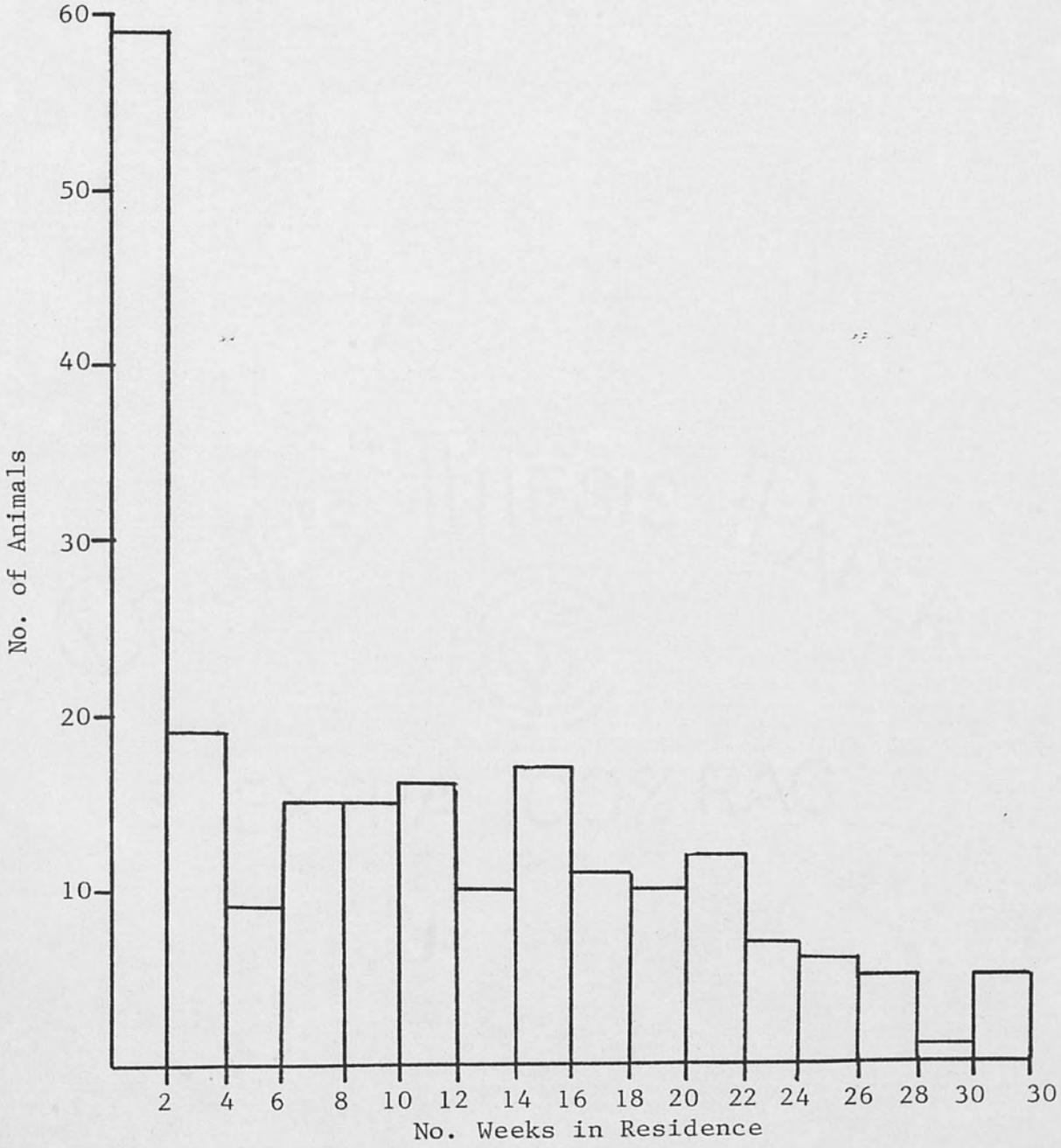

Fig. 6. Distribution of number of weeks in residence for beach mice on the beach grid.

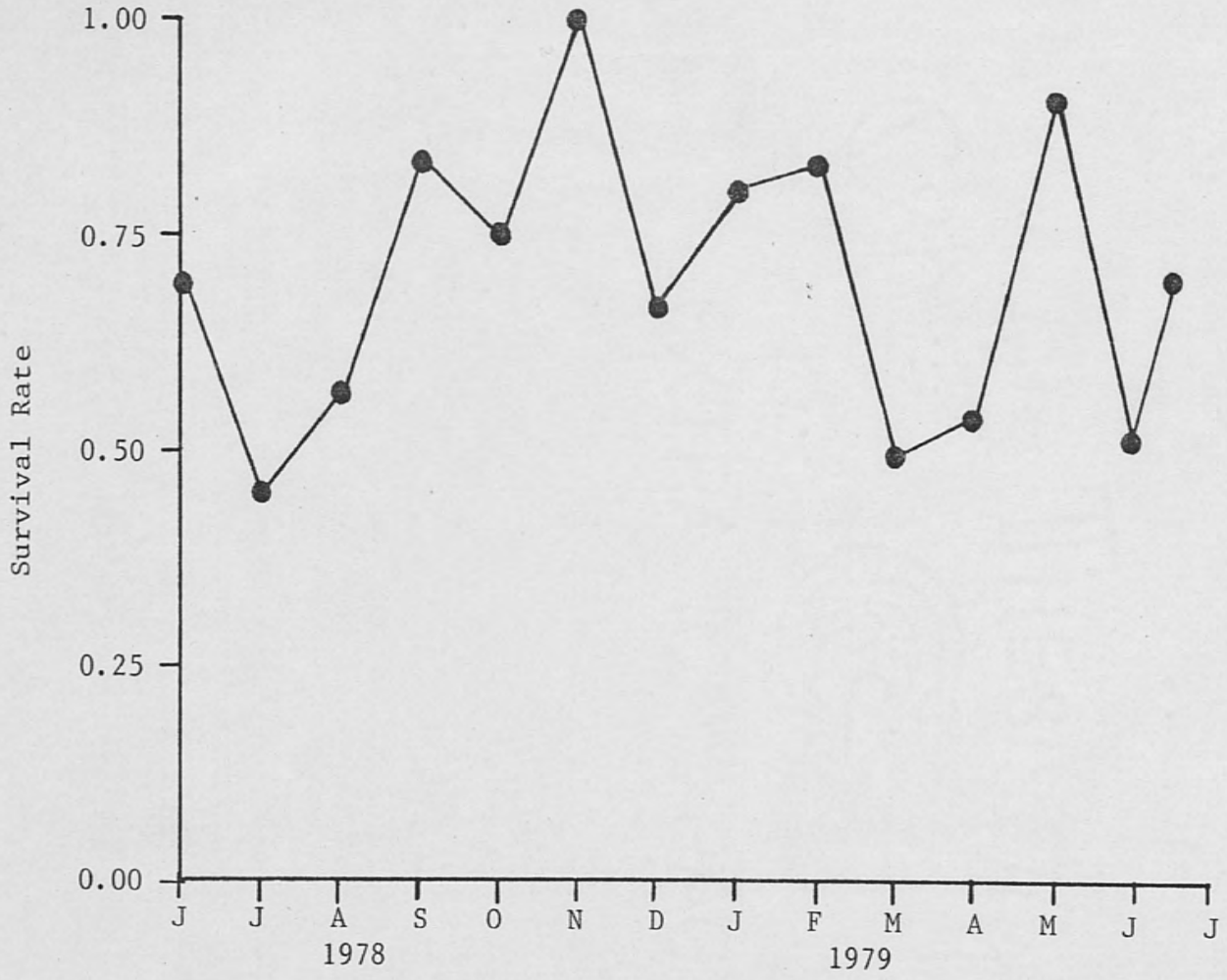

Fig. 7. Survival rates of beach mice on the dune scrub grid.

animals on the dune scrub was 7.5 weeks. Animals that were recaptured had an average length of residency of 11.6 weeks. Thus, beach mice on the dune scrub had a lower percentage of animals establishing residency than the beach grid, and residents on the dune scrub did not live as long (11.6 weeks) as residents on the beach grid (15.6 weeks).

Reproduction

External characteristics of male and female beach mice were used to assess the timing and intensity of reproduction over the period of unusual population increase. On the beach grid males with descended testes were observed in 13 of the 14 months of the study (Table 2). Following a period of low reproductive activity in July the proportion of males with descended testes increased in August (77%; n = 11), and peaked in September (100%; n = 7). The proportion of males with descended testes never exceeded 25% in the period from October 1978 through July 1979. Males with partially-descended testes were common in most months after September 1978. We do not know if these males were capable of breeding.

During the study 58 of 112 (52%) of the males entering the population on the beach grid were observed with either descended or partially-descended testes (Table 3). Animals recruited during the summer (90%) and fall (80%) were more likely to become reproductively active than winter (60%) and spring (30%) recruits. However, the number of reproductively active males (n = 35) was greater in the winter-spring period than in the summer-fall period (n = 17).

Table 2. Monthly proportions of males on the beach and dune scrub grids with descended and partially-descended testes (remaining proportion was abdominal). Sample sizes (N) in parentheses.

Month	Year	Beach grid			Dune scrub grid		
		Descended	Partially-descended	N	Descended	Partially-descended	N
June	1978	0.60	0.00	(5)	0.67	0.17	(6)
July		0.17	0.27	(11)	0.50	0.00	(2)
August		0.77	0.23	(9)	0.67	0.33	(3)
September		1.00	0.00	(7)	N.D.	N.D.	(0)
October		0.25	0.58	(12)	0.00	1.00	(1)
November		0.15	0.39	(13)	0.00	1.00	(3)
December		0.07	0.29	(14)	N.D.	N.D.	(0)
January	1979	0.10	0.16	(39)	1.00	0.00	(1)
February		0.17	0.36	(30)	0.25	0.25	(4)
March		0.09	0.15	(58)	0.00	0.60	(5)
April		0.05	0.28	(55)	0.00	0.33	(3)
May		0.08	0.23	(42)	0.00	0.12	(8)
June		0.02	0.35	(41)	0.00	0.50	(2)
July		0.00	0.16	(32)	0.00	0.17	(6)

Table 3. Numbers of males and females recruited on the beach and dune scrub grids by season and number and percentage of those recruits becoming reproductively active.

Season	Year	Beach grid					
		Males			Females		
		No.	No. breeding	(%)	No.	No. breeding	(%)
Summer	1978	10	9	(90)	5	3	(60)
Fall	1978	10	8	(80)	18	16	(89)
Winter	1978	40	24	(60)	44	24	(55)
Spring	1979	36	11	(30)	30	7	(23)
Summer	1979	16	6	(38)	9	0	(0)

		Dune scrub grid					
		Males			Females		
		No.	No. breeding	(%)	No.	No. breeding	(%)
Summer	1978	7	6	(86)	8	4	(50)
Fall	1978	2	2	(100)	1	1	(100)
Winter	1978	4	2	(50)	6	5	(83)
Spring	1979	12	3	(25)	9	4	(44)
Summer	1979	4	1	(25)	2	0	(0)

Female reproductive activity as indicated by enlarged mammaries occurred in 13 of 14 months with a peak in September and October (Table 4). The proportion of females with enlarged mammaries decreased steadily from November 1978 (62%) until July 1979 (0%).

Among females recruited on the beach grid 47% (50 of 106) were observed to have enlarged mammaries (Table 3). Most fall recruits (89%) were incorporated into the breeding population and surely contributed to the continued population growth. As was the case with males a smaller percentage of recruits from the winter (55%) and spring (23%) were breeding, but the total number of females from the winter (24) that became reproductively active was greater than during the fall (16).

Reproductive activity of male beach mice on the dune scrub grid appeared to follow the pattern observed on the beach grid (Table 2). Small sample size does not permit a critical analysis; however, it was apparent that males with either partially-descended or descended testes were present in most months. A depression of activity in winter and spring was consistent with findings from the beach grid. Males recruited on the dune scrub grid often entered the breeding population (48%) and with the greatest frequency in summer (6 or 7) and fall (2 of 2) (Table 3).

Females with enlarged mammaries were present on the dune scrub grid in 12 of 14 months (Table 4). A greater proportion of the females on the dune scrub grid were engaged in breeding during the winter and spring months than on the beach grid. Females recruited on the dune scrub were more likely to breed during the winter (83% vs 55%) and

Table 4. Monthly proportions of females on the beach and dune scrub grids with enlarged mammaries. Sample sizes in parentheses.

Month	Year	Beach grid	Dune scrub grid
June	1978	0.20 (5)	0.00 (5)
July		0.00 (5)	0.33 (3)
August		0.50 (6)	0.50 (2)
September		1.00 (5)	1.00 (1)
October		0.90 (10)	N.D. (0)
November		0.62 (16)	0.33 (3)
December		0.54 (24)	1.00 (3)
January	1979	0.52 (54)	1.00 (1)
February		0.38 (35)	0.71 (7)
March		0.29 (65)	0.50 (2)
April		0.27 (64)	0.80 (5)
May		0.17 (36)	0.50 (10)
June		0.06 (31)	0.40 (5)
July		0.09 (21)	0.00 (6)

spring (44% vs 23%) than animals on the beach grid (Table 3).

Age Structure and Sex Ratios

Age classification of beach mice based on pelage is not as precise as desired, but alternative methods, for example body weight criteria, are equally arbitrary. With this in mind, the age structure of beach mice on the beach grid is indicated in Table 5. Adults predominated in the summer months of 1978 and 1979. The proportion of juveniles and subadults increased from October to a peak in December 1978. This recruitment was correlated with the timing and intensity of reproduction by resident adults.

Sex ratios of beach mice on the beach grid were not significantly different from 50:50 in any month according to chi-square tests ($p > 0.05$). A total of 116 males and 111 females were captured.

The age structure of beach mice on the dune scrub grid was similar to that of the beach population, but there were some notable differences (Table 5). Juveniles were identified in only one month, March. Subadults were recruited in two waves, one in November-December and a second from April through June. In general, the population on the dune was composed of a greater proportion of adults than was the case with the beach population.

Sex ratios of the dune scrub population were not significantly different from 50:50 in any month according to chi-square tests ($p > 0.05$). During the study 29 males and 26 females were captured.

Table 5. Age structure, as revealed by pelage class, on the beach and dune scrub grids. Numbers given are the proportions in each age class. Sample sizes in parentheses.

Year / Month	Beach grid			Dune scrub grid		
	Juveniles	Sub-adults	Adults	Juveniles	Sub-adults	Adults
1978						
June	0.00	0.00	1.00 (10)	0.00	0.00	1.00 (12)
July	0.00	0.00	1.00 (15)	0.00	0.00	1.00 (5)
August	0.00	0.07	0.93 (15)	0.00	0.00	1.00 (5)
September	0.00	0.00	1.00 (12)	0.00	0.00	1.00 (1)
October	0.00	0.18	0.82 (22)	0.00	1.00	0.00 (1)
November	0.03	0.28	0.79 (31)	0.00	0.17	0.83 (6)
December	0.10	0.24	0.66 (41)	0.00	0.33	0.67 (3)
1979						
January	0.04	0.17	0.79 (96)	0.00	0.00	1.00 (2)
February	0.05	0.09	0.86 (67)	0.00	0.00	1.00 (11)
March	0.03	0.06	0.91 (124)	0.15	0.00	0.85 (7)
April	0.02	0.15	0.83 (119)	0.00	0.12	0.88 (8)
May	0.00	0.06	0.94 (79)	0.00	0.06	0.94 (18)
June	0.00	0.07	0.93 (73)	0.00	0.15	0.85 (7)
July	0.00	0.04	0.96 (53)	0.00	0.08	0.92 (12)

Body Weight and Season

The body weights of male beach mice are indicated in Figure 8. Mean monthly weights of males were not significantly different over the period of the study ($p > 0.05$). Average weights clumped around 15 g. During the period of fall and early winter recruitment, variation in body weights of males reflected the input of younger and smaller individuals. No depression of mean body weight was apparent over the period of population increase and decline (Fig. 2 and Fig. 8).

Small sample sizes precluded a meaningful analysis of male body weights on the dune scrub grid.

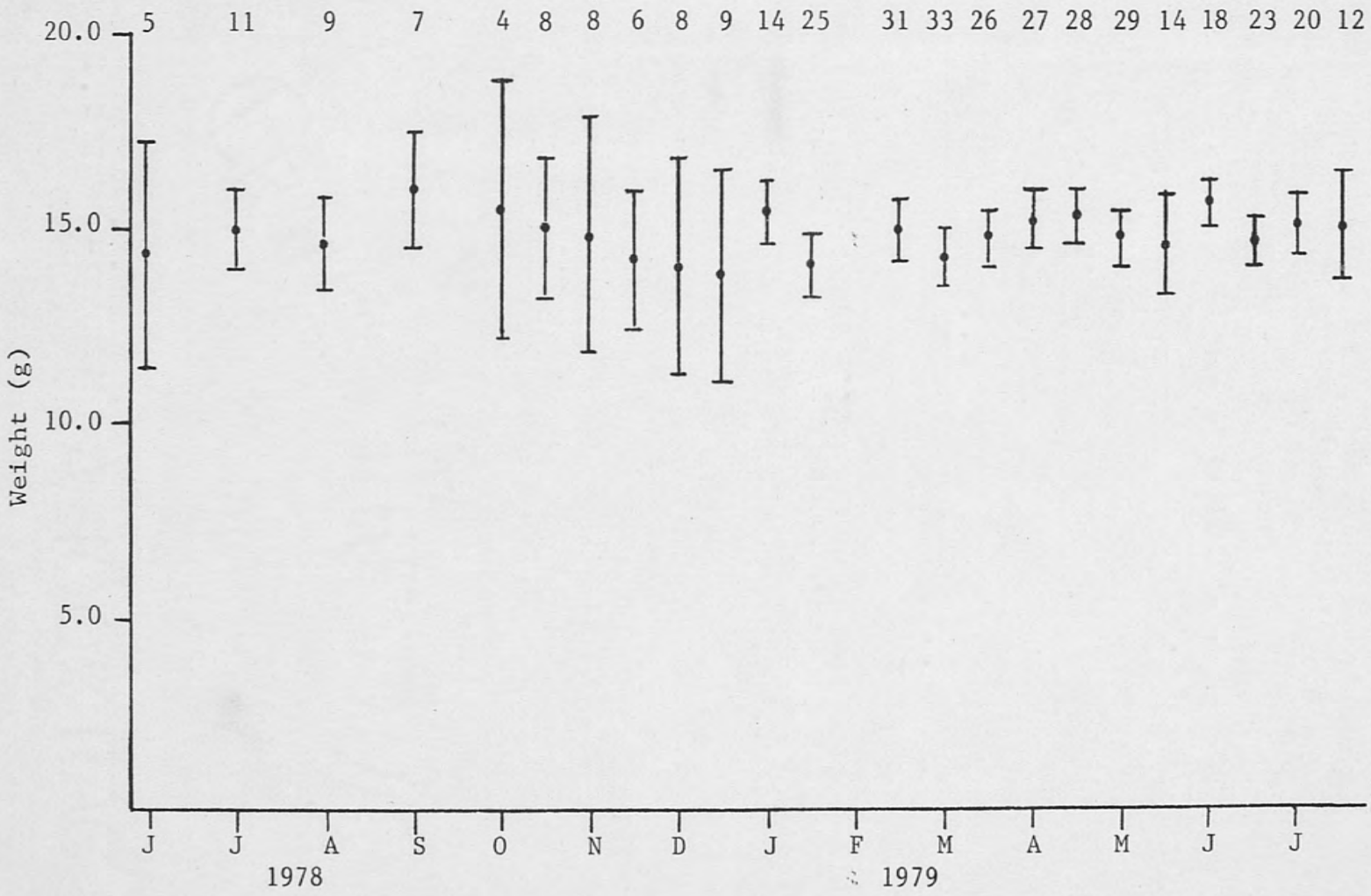

Fig. 8. Average weights of males on the beach grid. Brackets enclose 95% confidence intervals. Sample sizes are given at the top.

DISCUSSION

Reliability of Population Estimates by the Minimum Number Method

Estimates of population sizes were based on the minimum number known to be alive (Krebs, 1966). Hilborn et al., (1976) have shown that this method underestimates the actual trappable population size under conditions of low survival rates, low individual trappability, low trappability of new animals or high variance of individual trappabilities. The observed high survival between trap periods ($\bar{x}$ = 81%) on the beach grid was favorable to enumeration, whereas two parameters that could have led to an underestimation of population size were low individual trappability ($\bar{x}$ = 55% for females and $\bar{x}$ = 44% for males) and apparent low trappability of new animals, based on our inability to capture many immature individuals. Some of these limitations were alleviated by changing the trapping interval from monthly to biweekly. However, actual population size, especially during the time of heavy reproductive activity, was undoubtedly higher than the estimates.

On the dune scrub grid survival ($\bar{x}$ = 70%) and individual trappability ($\bar{x}$ = 34% for females and $\bar{x}$ = 35% for males) were lower than on the beach grid. These facts, along with our apparent inability to capture immature animals, and trapping at monthly intervals, leads me to conclude that minimum number estimates on the dune scrub grid were not as reliable as those on the beach grid. However, beach mouse popula-

dions were clearly different between the two habitats, and underestimation of actual trappable population sizes was not serious enough to jeopardize the credibility of my conclusions.

Varations in Densities of Peromyscus sp.

Terman (1968) summarized reports on density of Peromyscus sp. and commented that variation between seasons and among years was slight. Essentially the same conclusion was reached by French et al. (1975) in their review. Only rarely have unusually high densities of Peromyscus been reported. However some authors do allude to unusual population growth (2-3 year intervals) in association with abundant food (Miller and Getz, 1977). More typically, Peromyscus sp. have been regarded as classic examples of a k-selected life history strategy (Christian, 1970). The generally accepted explanation for the observed relative stability is some manner of self-regulation (Lidicker, 1978). However Peromyscus polionotus was singled out by Terman (1968) as exhibiting more seasonal and between year variation than other species of Peromyscus.

Varation in Densities of Peromyscus polionotus

A considerable range of peak densities has been indicated for P. polionotus: 21/ ha (Rand and Host, 1942); 3.5/ ha (Blair, 1951); 49.4/ ha (Caldwell, 1964); 21/ ha (Davenport, 1964); 14/ ha (Golley et al., 1965); 9.4/ ha (Gentry, 1966), and 173.8/ ha (Smith, 1968b). Smith's result was from a combination of live trapping and burrow excavation

in a small field (0.3908 ha) surrounded by natural vegetation. His total trap revealed density was 39.3/ ha (9.8/ ha of juveniles and 29.5/ ha of adults). The remaining animals (134.5/ ha) were lactating females and juveniles found in the burrows and not a part of the trappable population.

Densities of beach mice recorded on the dune scrub were well within the range of values given in the literature. In contrast, the peak density observed on the beach grid (67.0/ ha) was unusually high relative to published data on P. polionotus and other species of Peromyscus (Blair, 1951; Caldwell, 1964; Terman 1968). Furthermore, the population density was greater than 50/ ha for at least 4 months (Fig. 2). The density estimates were reliable for these reasons: (1) The estimate of density was based on the minimun number known to be alive. The inherent error was most likely to lead to an underestimation rather than an overestimate of density (Hilborn et al., 1976), particularly because of the bias against live trapping very young individuals (Gentry, 1966; Smith, 1968b). (2) Average individual trappability of mice whose captures were on the peripheral parts of the grid was not different from trappability of mice captured in the central parts of the grid. (3) No "edge effect" in terms of total captures was discovered. (4) Individual movements as measured by mean distance between successive captures were relatively modest (Extine, unpublished). The latter three points support the dicision to calculate density on the basis of an effective trapping area of 1.44 ha.

Seasonal variation in density was most pronounced on the beach

grid. Densities there during the summers of 1976-78 were very similar (Keim, 1979; Stout, 1979), but in 1979 the density was 38.0/ ha, almost a threefold increase over the previous three summers' densities. The difference in average densities between springs of 1978 (12.3/ ha) and 1979 (59.7/ ha) was particularly striking. In contrast to the variation observed on the beach grid, numbers of beach mice on the dune scrub grid were relatively stable. The increase in density from the fall of 1978 to the peak in spring 1979 was less than threefold Table 1).

Causes of Variation in Abundance

The unusual growth of the beach mouse population on the beach grid had its basis in changes in reproduction, survival and dispersal, all of which were favorable to growth. These same demographic events were either not in evidence or temporally delayed on the dune scrub grid.

Females on both study areas typically began to show evidence of reproduction in July or August. A depression in reproductive activity usually occurs in June and/or July. Thus, the annual breeding season extended from mid-summer until the winter months (Keim, 1979; Stout, 1979). Exact length of the breeding season is variable in that both onset and termination appear to be determined by proximate factors unique to years and grids.

The length of the breeding season on the beach grid in 1978-79 was extended relative to the previous two years. Keim (1979) found no evidence of male reproductive activity after October in 1976. Females

with enlarged nipples were observed until January 1977. Likewise, females ceased to breed in January of 1978 (Stout, 1979). In contrast, male and female reproductive activity in 1978-79 was somewhat delayed in onset, but extended until the study ended in July 1979.

The extended breeding season in 1978-79 appeared to result from in situ recruitment, rapid attainment of sexual maturity, and excellent survival of breeding age animals. Large proportions of new recruits entered the population in 1978-79 relative to previous years (Stout, 1979). For example, between September 1976 and April 1977, 82 new animals were captured and 43.9% of these were recaptured. The remaining individuals dispersed, died, or avoided recapture. During the same period in 1977-78, 48 new animals were captured and 45.8% were later recaptured. In striking contrast to these data, 164 new animals were captured between September 1978 and April 1979. Of these recruits, 73.2% were recaptured. Either dispersal was reduced or survival improved relative to the previous years. Based on the very high survival I observed in 1978-79 (Fig. 4), I believe dispersal was not very important in these population adjustments. High recruitment rates combined with high survival rates, as was the case during exponential population growth, is indicative of very little dispersal (Fairbairn, (1977).

In summary, although the proportion of breeding animals declined after October 1978, the number the number breeding in the winter and early spring months outpaced the fall levels (Tables 3 and 4). Clearly, recruitment helped to account for this relationship.

My observations on population growth of P. polionotus on the beach grid indicate a substantial rate of increase ($r = 0.092$) that is higher than many r values reported for microtine rodents (Krebs and Myers, 1974). The growth potential of P. polionotus is further augmented by its rapid sexual maturation. Clark (1938) found females under laboratory conditions experienced their first estrus at 29.6 ± 0.5 days. Apparently successive generations of beach mice were recruited into the population and commenced breeding themselves. According to Smith and McGinnis (1968), litter size of P. p. subgrisieus is a function of season in north-central Florida. They found the largest litters in the winter months. If this generalization holds for the beach mice, individuals entering the breeding population from late season (fall) litters would further accelerate population growth by having larger litters than summer young.

Average body weights of male beach mice on the beach grid were not significantly different ($p > 0.05$) over the period of unusual growth and decline. These results are consistent with the hypothesis that food was not limiting the population growth during late 1978 and early 1979.

I cannot dismiss the possibility that the population growth of beach mice was related to the low numbers (0-3) of cotton rats and some form of competitive release. During the previous two minimum numbers of cotton rats on the beach grid varied from 3-12 (Keim, 1979; Stout, 1979). It is not known what form competition between these two species might assume. For example, cotton rats are primarily grazers (Fleharty and Olson, 1969; Fleharty and Choate, 1973) and should not

compete for food with the omnivorous beach mice. However, grass is not available on the part of the beach grid where cotton rats were primarily captured. Some overlap in diet may well have occurred, but I am doubtful that densities of either species were thereby limited.

Habitat and Abundance

Substantial differences in the timing and intensity of demographic events in populations of beach mice were observed between the beach and dune scrub study areas. The density of beach mice was higher in the beach habitat than in the dune scrub for all seasons and the exponential increase in abundance observed there during the winter and early spring of 1978-79 was not manifested on the dune scrub (Fig. 2). Survival and residency time were reduced on the dune scrub relative to the beach grid. Beach mice were recruited into the population on the beach grid for times faster than on the dune scrub (Fig. 3). Therefore, I conclude the dune scrub represented marginal habitat for the beach mouse during this period of study.

The marked difference in performance between the populations of beach mice on the two study areas probably reflected intrinsic differences in habitat quality. The grids were about 6 km apart and experienced similar climatic conditions. Beach mice co-occurred with cotton mice (Peromyscus gossypinus) and cotton rats (Sigmodon hispidus), however local distributions and population variations among the species were not related (Extine, in preparation).

Timing of population growth on the dune scrub was delayed relative

to the beach grid but not as great as had been observed in the previous two years. Keim (1979) found peak densities on the beach grid occurred in January-February 1977 whereas the peak was delayed until May on the dune scrub. The same pattern was repeated in 1977-78 (Stout, 1979). In 1978-79, owing to an extended breeding season on the beach grid, peak densities were not reached until March-April. On the dune scrub density increased slightly over the winter and peaked in May.

The later attainment of peak population density on the dune scrub relative to population growth on the beach grid may be explained by the arrival of immigrants from surrounding and relatively more optimal habitats. I suspect habitats near the coastal dunes to be a likely source area. However, dispersal was not the only source of recruits as breeding activity of residents was demonstrated (Tables 2 and 4). Trends in reproductive activity were similar on both grids in 1976-77 (Keim, 1979) and in 1977-78 (Stout, 1979). In 1978-79 there were reproductively active individuals on the dune scrub during most months of the study, however recruitment rate of individuals was low, especially during the late fall and winter months. Nevertheless, greater proportions of recruits became reproductively active during the winter months on the dune scrub than on the beach grid (Table 3). I conclude that immigration and late winter breeding by immigrants sustain the early spring peak in population growth and perhaps, ultimately, the persistence of the dune scrub population.

Regulation of Numbers in Peromyscus Populations

The regulation of abundance in Peromyscus populations has been the subject of considerable work in the last two decades. A complete review of this work will not be attempted here. Rather, I will summarize the major findings with regard to regulation of the species about which the most is known: Peromyscus maniculatus and P. leucopus. Given this background, regulation of abundance of P. polionotus niveiventris will be discussed.

Sadleir (1965) reviewed the early work on population biology of Peromyscus maniculatus. A number of factors was suggested as being important in control of abundance including predation (Blair, 1948; Howard, 1949; Brant, 1962) and cold weather in concert with food shortage (Howard, 1949). He concluded that the regular nature of the annual cycle of abundance suggested some manner of intrinsic regulation as opposed to extrinsic or enviornmental limitations. Sadleir (1965) showed that the decrease in aggressive behavior by males at the end of the breeding season coincided with increased survival and recruitment of young. These results were confirmed and extended by Healey (1967) who concluded that spacing behavior of resident males limited densities during the breeding season by preventing settling of immigrants and interfering with growth and survival of resident offspring.

A general model of population regulation of Peromyscus maniculatus was proposed by Petticrew and Sadleir (1974). During the reproductive season, breeding males limit their numbers by spacing behavior. Breeding males supress survival of all juveniles. However, recruitment of juveniles occurs rapidly at the end of the breeding season as male

aggression drops off. Therefore the highest number of animals may be expected at the end of the breeding season. Petticrew and Sadleir offer the length of the breeding season as a mechanism for regulating the number of females. During the non-breeding season they suggested that all deermice were regulated by survival. The longer the non-breeding period, the lower the densities would be at the beginning of the next breeding season.

Fairbairn (1977, 1978) confirmed the basic findings of Sadleir (1965) and Healey (1967) and further refined some elements of the basic model as stated by Petticrew and Sadleir (1974). For example, she found that the aggression of males at the onset of breeding resulted in dispersal of subordinate males. Fairbairn (1977) dealt more specifically with regulation of female abundance. She suggested that with regard to breeding age females, the interaction of spring weather, over-winter food supply, and the onset of the female breeding may be just as important as male aggression in determining breeding densities of Peromyscus maniculatus.

Population regulation of Peromyscus leucopus was first considered in detail by Metzgar (1971). He postulated that regulation was achieved by resident females excluding other females from their home ranges. Thus at low densities female home ranges were exclusive of other females. New females were able to establish home ranges in interspaces among residents. Eventually no more females could settle and an upper limit to their density was achieved. Males followed a pattern of dispersion similar to that of the females with an important

exception. At higher densities males continued to permit immigrant males to establish home ranges. Metzgar concluded that spacing behavior did not appear to set an upper limit on male density. All of Metzgar's data and inferences applied to the spring and summer breeding season.

Christian (1971) presented data on P. leucopus population which underwent an unusual period of growth in a grassland habitat. He did not provide a full demographic analysis, but some constrasts may be made with the findings of Metzgar (1971). Firstly, Christian had good evidence that females of the first litters were recruited and became reproductively active. This led to an accelerated population growth. Secondly, he concluded that inhibitation of reproduction was manifested near the end of the breeding season.

Myton (1974) studied spatial relations of P. leucopus in a Maryland woodlot. She concluded the "family" group was made up of an adult female and several adult males and a number of juveniles. A limited number of adult females is implied, corroborating the observations by Metzgar (1971).

Although not primarily concerned with population regulation, Miller and Getz (1977) presented a large body of data on P. maniculatus and P. leucopus in New England. They concluded, in close agreement with Petticrew and Sadleir (1974), that population densities achieved in a given year were closely related to the length of the non-breeding season. Also, Miller and Getz found both species of Peromyscus to show periodic peaks of abundance that correlated with natural food

availability.

Hansen and Batzli (1978, 1979) supplied food to P. leucopus populations in Illinois. They suggested that regulation of numbers must been considered as fundamentally different between the breeding and non-breeding season. During the breeding season density of adult females was found to be closely correlated with decreased survival and increased dispersal of young. This is basically the same conclusion reached by Metzgar (1971), but is incongruous with the model of Petticrew and Sadleir (1974) for P. maniculatus. Hansen and Batzli found density limits during the non-breeding season were determined by food supply and associated rates of survival.

Regulation of Numbers in Beach Mouse Populations

I propose to develop a general model or hypothesis for the regulation of numbers in beach mouse populations. The model is largely qualitative but is subject to critical testing and validation in the field.

Environmental factors such as climatic conditions, food supplies, and predation, singly or in combination, could have influenced population size. Thus the unusual increase in abundance of beach mice may have resulted from the return to average climatic conditions in 1978-79. Previous winters of 1876-77 and 1977-78 had been characterized as rather colder than average. Food supplies may have varied among the years and led to the variation in numbers of beach mice. Food always seemed abundant on the beach grid but direct measurements of food avail-

ability were not made. Therefore, I can only speculate that food was not limiting. The fact that many recruits to the population during the winter of 1978-79 were observed in reproductive condition supports the view that food was not limiting in that year. Lastly, predation pressures may have accounted for depressed growth in some years. I have no direct evidence that this was the case. Regardless of the exact mechanism involved, densities were observed to reach unusual levels the winter and early spring of 1978-79. A corollary to this conclusion is that tight regulation of abundance as predicted for Peromyscus was not operative.

A number of studies have shown that density regulation of Peromyscus operates via social behavior as a negative feedback on reproduction (Christian, 1971 and literature cited therein). Lidicker (1965) has shown that several species of Peromyscus, when maintained in larger enclosures, do exhibit an asymptotic state of growth even in the presence of abundant food and water. Terman (1965, 1973) found that animals which failed to breed under asymptotic conditions could indeed breed when removed from these conditions. The question is why did P. polionotus not follow this pattern and shut off reproductive activity as the buildup in density occurred in the winter of 1978-79?

Several possibilities exist to explain this observation. A density-dependant negative feed-back on reproduction may not be well developed in beach mice. The lack of a distinct breeding season in these mice shows them to be very plastic with respect to environmental conditions suitable for breeding. Lastly, the social system of the

beach mouse may lend itself to growth and tolerance of high densities.

The social system of the beach mouse is based on a male and female with or without their young in a burrow (Smith, 1967a). During the breeding season P. Maniculatus and P. leucopus are not found in pairs but rather occupy individual home ranges which overlap to some extent (Stickel, 1968; Madison, 1977). The vicinity of a nest with young is probably defended by the female of most Peromyscus (Stickel, 1968). However the areal extent of this defended area (territory) is not known (Hill, 1977). Based on radiotelemetry and live trapping, Madison (1977) indicated that home ranges of male and female P. leucopus were generally not overlapping and that overlap of home ranges between members of the same sex was modest. If one assumed home ranges of P. leucopus and P. polionotus were of a similar size, a greater density of breeding animals would be tolerated by P. polionotus owing to the pairing of individuals.

The response of resident animals to settling of immigrants is an important feature of the dynamics of space tenure and the question of density regulation (Krebs, 1970; Davies, 1978). Further insight into the relationship between the social system of Peromyscus and population regulation may be gained by an analysis of resident abundance and overall population levels. Such an analysis was done by Metzgar (1979) in a study of P. maniculatus. He found very little variation in the number of Old-2 animals (animals known to have been alive on the study area for at least two months) despite a considerable increase in total density. I reanalyzed his data and found no correlation between total

numbers of males and females and the number of Old-2 males and females ($r = 0.069$ and $r = 0.486$ for males and females, respectively). A similar analysis of my data revealed highly significant correlations for both males ($r = 0.898$; $p < 0.01$) and females ($r = 0.791$; $p < 0.01$). Thus many new individuals remained on the beach grid and achieved Old-2 status, contrary to Metzgar's findings. During March and April 1979, the time of peak population density, Old-2 individuals accounted for over half of the total number of males and females. This compares with approximately 25% found by Metzgar (1979). Furthermore, the number of Old-2 animals was not stable, as found by Metzgar. In my population the number of Old-2 males increased from 3 in July 1978 to 31 in May 1979, and Old-2 females increased from 2 in November 1978 to 32 in April 1979. These differences in the accumulation of resident individuals between P. maniculatus and P. polionotus suggest a greater tolerance to large numbers of breeding age individuals of both sexes by the beach mouse.

I conclude that selective pressures to evolve mechanisms for limiting population growth have not been very strong in the evolutionary history of P. p. niveiventris. An examination of evidence regarding two limiting factors, home sites and food, may support this conclusion. The rather general requrements for burrow sites on the dunes (Hayne, 1936; Smith and Criss, 1967) suggest that home sites are seldom if ever limiting for the beach mouse. A similar argument may be assumed with respect to food, owing to the fact that beach mice are omnivorous (Smith, 1966). My guess is that the bulk of the diet is

seeds with the option to take animal material in an opportunistic fashion. Seasonal variations in variability of food items may be avoided by food storage, although I have no evidence that this is true. Under some circumstances food may be limiting. Smith (1971) found that P. polionotus does respond to supplementary food by increasing in density. This suggests that densities were not limited by social behavior independant of food supply and that populations may indeed be limited on occasion by food.

Small body size of P. p. niveiventris is another feature which may contribute to a tolerance of high density. I believe that small body size is primarily an adaptation to burrowing. It is an advantage however in terms of the interplay between food requirements and density limitations. Small size (biomass) allows a much greater number (density) of individuals to exist because of the lower food consumption per individual. Eisenberg (1980) more completely develops this subject.

P. polionotus may undergo torpor on a daily basis (Extine and Evans, personal observation). Smith and Criss (1967) have shown that diel body temperatures of P. polionotus are lowered during the day with an attendant reduction in oxygen consumption. This behavior is adaptive in that energy demands are reduced per individual and more individuals may be maintained per unit area.

Beach mice in general and P. p. niveiventris specifically are typically the dominant small mammal in coastal dune environments. Competition for food resources with other small mammals or other taxa in the seed eating guild does not appear to be of much consequence.

For example, ants and seed eating birds occurred at very low densities on the beach grid. Ants were, however, a more conspicuous part of the seed eating guild on the dune scrub grid. Gentry and Smith (1968) concluded that in South Carolina P. polionotus was in direct competition with ants (e.g., Pogonomyrmex badius) for seed resources in old fields. In general, I conclude that diffuse competition (Pianka, 1974) was not a factor in limiting the number of beach mice on the beach grid; conversely, competition may have been relatively more important on the dune scrub site.

Dispersal is now regarded as a key factor in the regulation of abundance of small mammals (Krebs, 1978). Garten and Smith (1974) have suggested that dispersal is an important population regulating mechanism for P. polionotus, especially during the time of increased population growth. My data from the beach grid do not support this conclusion. During the period of rapid growth (i.e., high recruitment) survival was very high, indicative of little dispersal (Fairbairn, 1977). I have argued earlier that dispersal into marginal habitats, e.g., the dune scrub, does occur. Thus, I must conclude that dispersal is not necessary for population regulation of P. p. niveiventris.

In summary, self-regulation of numbers of P. p. niveiventris is poorly developed relative to other Peromyscus. My evidence indicates that density dependant reproductive inhibition is not well developed for beach mice. In contrast to other Peromyscus, spacing behavior does not appear to be an effective regulator of density in beach mice. Population growth and densities achieved appear to be more a result

of extrinsic factors such as food and local weather conditions. Under favorable environmental conditions the reproductive potential of P. p. niveiventris (litter size, post-partum estrus, rapid sexual maturity, recruitment of young into the breeding population, and variable length of breeding season) leads to rapid population growth and the attainment of high densities. Dapson (1979) reached similar conclusions with respect to the reproductive potential of P. p. phasma, the beach mouse found on Anastasia Island, Florida. In addition, the highly social nature of P. p. niveiventris (e.g., monogamous breeding system) contributes to the tolerance of these occasional high densities.

SECTION II. DISPERSION, MOVEMENTS, AND HABITAT OCCUPANCY

INTRODUCTION

The beach mouse (Peromyscus polionotus) occupies portions of the narrow band of coastal dune and coastal strand vegetation on Florida's east and west coasts and a limited section of the Gulf coast of Alabama (Ivey, 1949; Blair, 1951; Bowen, 1968). A complex gradient of physical and biological factors imposes marked changes in the species composition and physiognomy of these plant communities from the coast progressing inland. At a particular site these changes may occur within a few meters. Thus, coastal dune vegetation is heterogeneous or patchy, often both parallel and perpendicular to the shoreline. The occupancy of patchy environments by animal populations has been discussed by MacArthur and Pianka (1966) and reviewed by Wiens (1976).

During the winter and spring of 1978-79, I observed an exponential population increase in the beach mouse, Peromyscus polionotus niveiventris, in a Florida beach habitat. An unusually high density (67/ha) was reached and population density remained high (> 50/ha) for almost four months. Average density for the two years prior to this study had been 13.4/ha. The demographic parameters of this increase were discussed in an earlier paper (Extine and Stout, manuscript). In this paper, I will deal with the dispersion patterns of beach mice during the different phases of population growth. Here I define dispersion as the local distribution of mice on the grid, and not as individual spatial arrangement (Metzgar, 1979,1980).

The study area contained three distinct bands of vegetation running parallel to the beach. My first objective is to examine the distribution of captures in the three vegetative zones during the different phases of population growth. If beach mice do not display habitat preferences then the proportion of captures in each zone should be equal, regardless of density. If, on the other hand, the mice do not treat the grid as homogeneous, this should be reflected in the distribution of captures. In addition, a population shift into suboptimal portions of the grid, if any are present, should occur as density increases (Brown, 1969; Fretwell and Lucas, 1969).

My second objective is to discuss the movements of beach mice during the different phases of population growth. Many investigators have shown that home range size of Peromyscus sp. is inversely density-dependent (Pearson, 1953; Stickel, 1960; Brant, 1962; Shure, 1970). However, Davenport (1964) found that home range sizes of P. polionotus showed little relationship to seasonal changes in population density. My data were not appropriate for calculations of individual home range size, but analysis of movements in relation to population density may help to clarify local distibution and habitat shifts.

MATERIALS AND METHODS

Description of Study Area

The study area was located on the north end of the Canaveral Peninsula portion of Merritt Island, Brevard Co., Florida, USA. The grid was immediately adjacent to the high tide mark and extended inland over two minor dune lines, a major dune (6 m above sea level), and 30 m beyond the crest of the major dune line. Three obvious zones of vegetation ran parallel with the beach and dune lines. Zone 1 was the most seaward and was covered primarily with sea oats Uniola paniculata, sunflower Heterotheca subaxillaris, and morning glories Ipomoea stolonifer and I. pes-caprae. Zone 1 varied in width from 40-50 m. Zone 2 was located between zone 1 and the major dune line. Much of this zone was bare sand with clumps of palmetto Serenoa repens, a few sea grape Coccoloba uvifera, and buckthorn Bumelia tenax. Gopher apple Licania michauxii formed extensive mats in some places. Zone 2 was approximately 45 m in width. Zone 3 began at the top of the major dune line and extended inland for several hundred meters. It consisted of a dense shrub layer. Palmetto and sea grape were most abundant and wax myrtle Myrica cerifera, buckthorn and snowberry Chiococca alba were common but scattered. There was almost no ground cover beneath the shrubs but a heavy litter was present. The grid extended about 30 m into zone 3.

Vegetation Sampling and Analysis

Three zones of vegetation were subjectively identified on the trapping grid. Sample points were randomly located within each zone: 9 for zone 1 and 6 for zones 2 and 3. Line transects 15 m in length were examined and the canopy coverage of each plant species intercepted was recorded to the nearest cm (Daubenmire, 1968). By this procedure, the canopy coverage may exceed the absolute length of the transect due to superposition of plants. The plant data were reduced to yield absolute and relative coverage, frequency, and relative frequency as described in Mueller-Dombois and Ellenberg (1974: 111-120). Importance values (IV) for the species were the sum of relative frequency and relative coverage.

The areas on the trapping grid occupied by each zone differed slightly. Approximately 5000 m^2 of the grid was occupied by zone 1, 5400 m^2 by zone 2, and 4000 m^2 by zone 3. Due to these differences, the data for captures has been expressed on an assumed hectare basis to permit easy comparison. However, these comparisons must be viewed with some caution since the boundaries of each zone were quite different. For example, zone 1 had 90 m of boundary with non-grid zone 1 community and 120 m along the non-habitable region of open beach. The grid region identified as zone 2 bounded similar vegetation along 90 m. However, because the grid extended into a large homogeneous region of zone 3, there was 180 m of border which connected directly to zone 3 community. Thus, there was the greatest possibility of an "edge effect" in zone 3 of the grid.

Trapping Procedures

The study area consisted of 64 trap stations arranged in an 8 X 8 pattern (1.44 ha) with trap stations 15 m apart. The grid was set up in 1975 and, prior to my study, had been trapped monthly since July 1976 (Keim, 1979; Stout, 1979). Single Sherman live traps (8 x 9 x 23 cm) were placed within 1-2 m of each trap station. When overall trap success exceeded 50% of the original 64 traps, 56 extra traps were added to ensure a surplus of traps (Krebs et al., 1976). Extra traps were placed on the columns half-way between the trap stations. All traps were opened during the afternoon, baited with oat flakes, and checked for captures the following morning. The grid was trapped at monthly intervals from June 1978 through September 1978 and at approximately two week intervals from October 1978 to July 1979.

P. polionotus were marked with numbered monel ear tags, sexed, classified as juvenile, subadult, or adult by pelage characteristics and weighed with a Pesola spring balance. Reproductive status of males was determined by position of the testes: abdominal, partially-descended, or descended. Female reproductive status was determined by the condition of the vagina (perforate or imperforate), mammaries (small or enlarged), and the symphasis pubis (closed or notched). Mice were released at the point of capture.

RESULTS

Vegetation

Plant cover of zone 1 was nearly continuous but not dense. Twelve species with an importance value ≥ 5.0 were detected by line transects (Table 1). The leading dominants were camphor weed Heterotheca subaxillaris (IV = 34.4) and sea oats Uniola paniculata (IV = 23.9). Four species, including Heterotheca and Uniola, were shared by zones 1 and 2. Saw palmetto Serenoa repens was the leading dominant (IV = 72.7) in zone 2. Serenoa and sea grape Coccoloba uvifera were found in zones 2 and 3. All the plant species found in zone 3 with an IV ≥ 5.0 were shrubs.

Canopy coverage of herbs, grasses, and shrubs recorded in each zone provides a convenient summary of vegetative differences (Table 2). Grass and herb coverage decreased markedly from zone 1 to zone 2; grass and herbs were inconspicuous in zone 3. Shrub coverage showed the opposite trend and accounted for 99% of the coverage in zone 3.

Beach Mouse Densities

I have previously discussed the changes in beach mouse numbers over the period of the study (Part I of this series). For the purposes of this paper it is only necessary to establish the relative magnitude of changes in minimum numbers associated with phases of population growth and decline (Table 3).

Table 1. Importance value of plants in zones 1, 2, and 3. Importance values were based on relative coverage and relative frequency and have a maximum value of 200. Values were based on line transects 15 m in length (9 lines in zone 1 and 6 lines in zones 2 and 3). Plants with an importance value < 5.0 are not listed.

	Importance value (%)		
Species	Zone 1	Zone 2	Zone 3
Heterotheca subaxillaris	34.4	11.8	
Uniola paniculata	23.8	10.8	
Ipomoea stolonifer	19.3		
Panicum amarulum	16.9		
Atriplex arenaria	16.2		
Andropogon virginicus	15.8	6.9	
Paspalum vaginatum	10.0		
Croton punctatus	9.4	10.0	
Ipomoea pes-caprae	9.1		
Sesuvium maritima	8.6		
Canavalia rosea	7.5		
Chloris petraea	5.5		
Serenoa repens		72.7	85.3
Coccoloba uvifera		31.7	18.1
Smilax auriculata		14.7	
Opuntia compressa		10.8	
Licania michauxii		7.0	
Myrica cerifera			28.1
Bumelia tenax			26.5
Chiococca alba			23.9
Myrcianthes fragrans			6.8

Table 2. Total plant coverage (cm) recorded on randomly located line transects (15 m per transect) in zones of vegetation found on the beach grid.

Zone	No. transects	Coverage (cm)			
		Herbs	Grass	Shrubs	Total
1	9	1589[a]	1316	547	3452
2	6	362	129	2625	3116
3	6	65	0	9210	9275

a Coverage values for zone 1 have been multiplied by 0.667 to make them comparable to zones 2 and 3.

Table 3. Average of minimum numbers of beach mice during four phases of population growth. Sample sizes in parentheses.

Phase of population growth	Mean of minimum numbers (no./ha)	Standard error
Stable (June-Nov. 1978)	13.7 (n = 8)	0.76
Exponential (Dec.-Feb.1979)	37.3 (n = 5)	7.37
Peak (March-April 1979)	65.4 (n = 4)	1.07
Decline (May-July 1979)	41.9 (n = 5)	3.49

Dispersion

Total captures and vegetative zones.— Because I could easily identify three distinct vegetative zones on the grid, total captures were broken down according to zone. Of the 769 total captures, 233 (30%) occurred in zone 1, 301 (39%) in zone 2, and 235 (31%) in zone 3. Although only 31% of the captures were in zone 3, its area (0.40 ha) was smaller than that of zone 2 (0.54 ha), or zone 1 (0.50 ha). Capture success, defined as the number of captures divided by the number of trap nights, was actually higher in zone 3 (0.408) than in zone 2 (0.348) or zone 1 (0.306). If I assume that the proportion of total captures in a zone is a function of the area of that zone relative to the total area, beach mice differed in their use of the zones (χ^2 = 6.98; $p < 0.05$) (Table 4).

First-captures, recaptures, and vegetative zones.— Total captures in each zone were further broken down into first-captures and recaptures (Table 4). More first-captures but fewer recaptures than expected occurred in zone 1. Zone 2 showed the opposite trend with fewer first-captures but more recaptures than expected. Zone 3 had both more first-captures and recaptures than expected. Distribution of first-captures (χ^2 = 8.85; $p < 0.025$) and recaptures (χ^2 = 20.26; $p < 0.005$) among the zones was significantly different from expected.

First-captures, age, and vegetative zones.— Analysis of first-captures by age (immature and adult) and vegetative zone, unadjusted for area, revealed that of the 68 individuals that were immature (juvenile or subadult) at first-capture 50% (34) were first caught in

Table 4. Number of total captures, first-captures, and recaptures by zone. Expected values were obtained by allowing for the proportion of the total area of each zone on the grid, and assumed no habitat preference. Percent of expected in parentheses.

Zone	Total captures		First-captures		Recaptures	
	Observed	Expected	Observed	Expected	Observed	Expected
1	233 (87)	267	92 (121)	76	141 (74)	191
2	301 (105)	288	62 (76)	82	239 (116)	206
3	235 (110)	214	65 (110)	59	170 (111)	153
χ^2	6.98; $p < 0.05$		8.85; $p < 0.025$		20.26; $p < 0.001$	

zone 1. This compares with 32% (22) in zone 2 and 18% (12) in zone 3. Of the 156 individuals that were adults at first-capture 38% (59) were first caught in zone 1, 27% (42) in zone 2, and 35% (55) in zone 3. The frequency of first-captures, adjusted for area, was significantly different among zones for both immatures ($\chi^2 = 7.58$; $p < 0.025$) and adults ($\chi^2 = 8.25$; $p < 0.025$). Thus, fewer immatures, but more adults than expected were first captured in zone 3. Also, a higher percentage of immatures than adults were first captured in zone 1.

First-captures, sex, and vegetative zones.— Analysis of first-captures by vegetative zone and sex revealed that the ratio of males to females was not significantly different ($p > 0.05$) from 1:1 ($\chi^2 = 0.681$, 0.803, and 0.914 for zones 1, 2, and 3, respectively). In zone 1, 54.2% of the first-captures were males, while in zones 2 and 3 males made up 55.7% and 44.3% of the first-captures, respectively.

Captures, phase of population growth, and vegetative zones.— In order to study the dispersion patterns of beach mice during the different phases of population growth, numbers of first-captures and recaptures per ha of vegetative zone were calculated for each trap period. These values were then combined into the following periods: stable population density (June- November 1978), exponential population growth (December 1978-February 1979), peak densities (March-April 1979), and declining densities (May-July 1979) (Table 3).

The average first-capture density in each zone was similar during both the periods of stable low density and exponential population growth (Table 5). However, during the periods of peak and declining densities first-capture density in zone 1 was much higher than the

Table 5. Average number of first-captures and recaptures per ha and ratio of first-captures to recaptures during the different phases of population growth. Standard errors are in parentheses.

Phase of population growth	Zone	First-captures	Recaptures	First-captures: recaptures
Stable densities	1	3.0 (0.69)	3.7 (1.05)	0.81
	2	3.0 (0.69)	7.4 (1.21)	0.40
	3	5.6 (1.74)	6.2 (0.69)	0.90
	$\bar{x}$	3.6 (0.62)	5.7 (0.69)	0.63
Exponential growth	1	12.4 (2.29)	8.0 (2.97)	1.55
	2	11.1 (2.34)	21.5 (5.84)	0.51
	3	12.3 (2.43)	19.3 (6.12)	0.63
	$\bar{x}$	11.8 (2.11)	16.2 (4.85)	0.73
Peak densities	1	13.0 (2.08)	29.0 (2.08)	0.44
	2	5.6 (1.31)	36.6 (2.31)	0.15
	3	9.4 (3.59)	31.9 (2.13)	0.29
	$\bar{x}$	9.2 (1.89)	32.6 (1.86)	0.28
Declining densities	1	7.3 (1.84)	14.7 (3.53)	0.49
	2	2.2 (0.57)	20.7 (1.99)	0.10
	3	4.2 (0.83)	22.9 (3.38)	0.18
	$\bar{x}$	4.5 (0.82)	19.2 (2.39)	0.23

other two vegetative zones, especially in zone 2. Density values for zone 3 may have been inflated owing to the small area on the grid and the fact that it was bounded on three sides by similar habitat, thus producing an "edge effect".

Average recapture density was greater in zones 2 and 3 than in zone 1 during all phases of population change (Table 5). Animals present on the grid for at least two weeks were considered residents. Thus, resident (recapture) density was greatest in zones 2 and 3 over the period of the study. During the period of exponential population increase, zones 2 and 3 increased in density 14.1/ha and 13.1/ha, respectively. In contrast, zone 1 increased only 4.3/ha. However, in the period of peak numbers, recapture (resident) densities were similar among the zones.

The ratio of first-captures to recaptures within zones was higher for zone 1 than zone 2 during all phases of population change and higher for zone 1 than zone 3 during all phases except for the period of stable low density (Table 5). First-capture density in zone 1 during exponential population growth (12.4/ha) was actually higher than recapture density (8.0/ha).

Residency, phase of population growth, and vegetative zones.— The zone of residency of animals known to be alive for two or more months was determined for the different phases of population growth and decline (Table 6). Animals were defined as residents in a zone if greater than 80% of their captures were in that zone. Animals with less than 80% of their captures in any one zone were given values of one-half for each zone they were captured in. By these criteria more animals

Table 6. Number of long-term residents associated with each zone during the different phases of population growth.

Phase of population growth	Zone	Number of individuals		
		Total	Males	Females
Stable densities	1	4	1	3
	2	11	6.5	4.5
	3	11	4.5	6.5
Exponential growth	1	15	5	10
	2	33	17.5	15.5
	3	30	11.5	18.5
Peak densities	1	21	7.5	13.5
	2	37	20.5	16.5
	3	30	12	18
Declining densities	1	17	7	10
	2	28	18.5	9.5
	3	24	11.5	12.5

were residents in zones 2 and 3 than in zone 1 during all phases of change in population density. As density increased more residents were associated with zone 1, but until the highest densities were reached most of the animals associated with zone 1 were also captured in zone 2.

The relative number of resident males and females differed among zones (Table 6). These differences were consistent over the phases of population growth and decline. For example, more females were resident in zone 1 than males. Males consistently outnumbered females in zone 2; whereas, the reverse was observed in zone 3.

Reproductive activity and vegetative zones.— A majority of the animals recruited into the population between June 1978 and February 1979 became reproductively active (65% of the females and 69% of the males). During this time period only 44% (4 of 9) of the females and 40% (2 of 5) of the males that were resident in zone 1 were reproductively active. This compares with 73% (11 of 15) of the females and 67% (14 of 21) of the males resident in zone 2, and 78% (14 of 18) of the females and 86% (12 of 14) of the males resident in zone 3.

Movements

Average distance between captures (ADBC) (Brant, 1962) was calculated for all individuals captured four or more times. The ADBC for individuals did not change as the number of captures increased, therefore all individuals of the same sex captured four or more times were combined. Males had a higher ADBC ($\bar{x}$ = 23.7 m; n = 37) than females ($\bar{x}$ = 18.7 m; n = 48) but this difference was not significant (t = 1.476;

$p < 0.20$).

Movements and phase of population growth.— Activity as measured by ADBC was evaluated within each phase of population growth. Movement distances of individuals were transformed as $\sqrt{x + 1}$ and averaged according to sex (Shure, 1970). The data revealed a non-significant shift ($p > 0.05$) to shorter recapture distances as the population changed from stable to exponential growth (Fig. 1). At peak densities recapture distances were not different from those of the exponential growth phase. During the decline phase movements of males increased slightly, but the trend was not significant ($p > 0.05$). In fact, no significant differences in movements of the sexes were revealed within any phase of population change ($p > 0.05$).

Movements and minimum numbers.— The ADBC was calculated for each trap period using all individuals (sexes combined) captured four or more times. These transformed values were plotted against the minimum number of beach mice known to be alive for the associated trap period (Fig. 2). No correlation was apparent between ADBC and minimum numbers ($r = -0.2683$; NS).

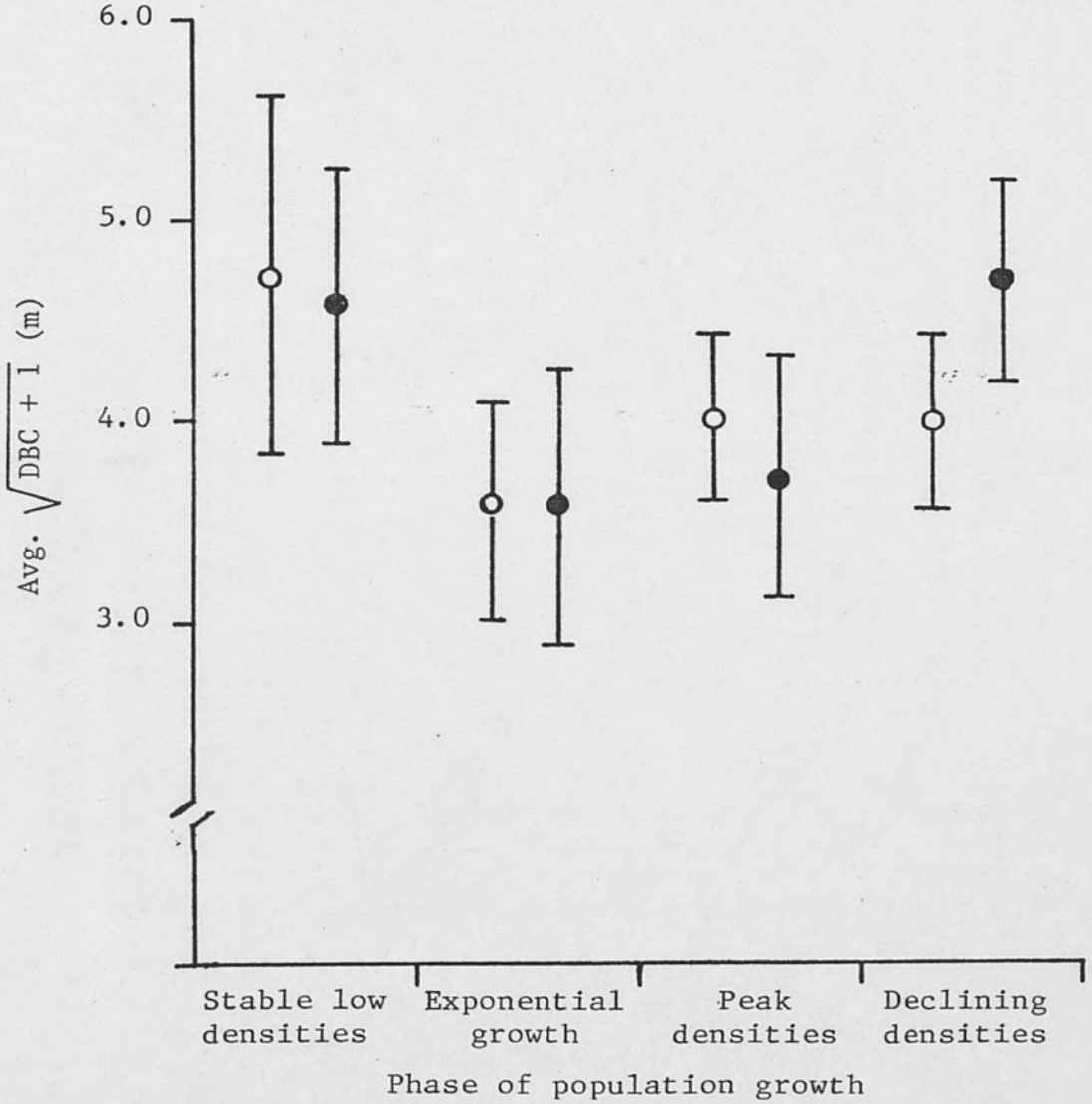

Fig. 1. Average distance between captures (ADBC) for males (●) and females (O) during the different phases of population growth. Lines enclose 95% confidence limits. Averages were obtained by taking the square root of the distance between captures (DBC) + 1 for all captures of residents during the different phases of population growth.

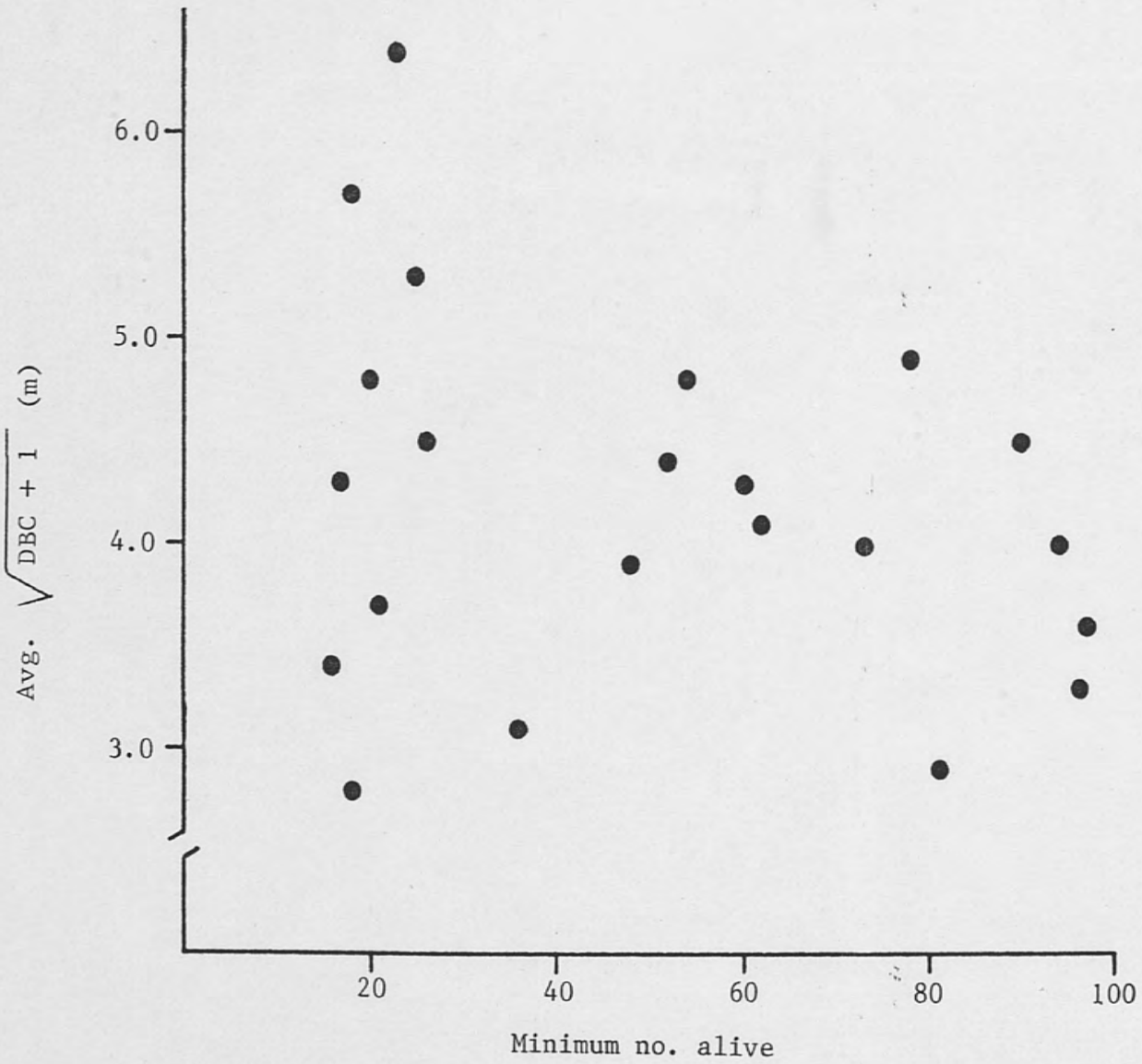

Fig. 2. Relationship between minimum number alive and average distance between captures (ADBC). ADBC values were obtained by averaging the square root of the distance between captures (DBC) + 1 for all resident captures in that trap period.

DISCUSSION

The results clearly showed that beach mice were not uniformly dispersed over the study area. Three vegetative zones, arranged contiguously and paralleling the coastline, were differentially occupied by the mice over a wide range of densities. First, I will discuss the implications of these dispersion patterns relative to the vegetative zones, phases of population growth, and residency. Finally, the shifts in habitat occupancy will be related to models of this phenomenon developed by Brown (1969), Fretwell and Lucas (1969), and Grant and Morris (1971).

Dispersion and Vegetative Zones

The local distribution of beach mice has not been examined beyond the most general comments found in papers by Ivey (1949) and Bowen (1968). The impression one formulates from these observations is that beach mice are restricted to the habitats occupied by sea oats. This was demonstrated not to be the case on the Canaveral Peninsula of Merritt Island (Keim, 1979; Stout, 1979). Rather, beach mice were found to be widespread beyond the limits of sea oats. Much of the variation or patchiness in the vegetative cover of the Canaveral Peninsula is represented on my study area (zones 1, 2, and 3; Tables 1 and 2). Therefore, a detailed analysis of dispersion patterns over a wide range of densities on the heterogeneous study area should provide insight

into patterns likely to be observed over much larger spatial units.

Stratification of total captures according to vegetative zone revealed the beach mice to be unevenly dispersed. Total captures in zones 2 and 3 exceeded expectations and in zone 1 fewer were observed than expected (Table 4). These results suggest that the habitats may be ranked in terms of quality as zone 2 ≥ zone 3 > zone 1. A reasonable alternative prediction based on the amount of grass and herb cover and associated food (Table 2) would have the ranking as zone 1 > zone 2 > zone 3. The observed lack of agreement with this hypothesis implies that food (grass and herbs) was not the major factor in the determination of local distribution of beach mice. Pitts and Barbour (1979) obtained similar results in their study on the microdistribution of Peromyscus maniculatus in a California beach habitat. However, neither my study nor Pitts and Barbour take into account the availability of arthropod prey among the vegetative zones on the study areas.

Division of total captures into first-captures and recaptures (Table 4) revealed uneven distribution among zones for both categories. More first-captures but fewer recaptures were recorded in zone 1 than expected, while the opposite trend was shown in zone 2. The frequency of first-captures and recaptures exceeded expectations in zone 3. These trends are consistent with the previous conclusion that zones 2 and 3 were better habitat than zone 1. If we consider recapture density to be an index to survival or residency time in a habitat we should observe more recaptures in the higher quality habitat (zone 2 ≥ zone 3 > zone 1).

First-captures in a zone were assumed to represent beach mice that

had been reared there or had immigrated. Zone 1 clearly yielded more first-captures than zones 2 or 3. I believe that this pattern resulted primarily from the local movement of young animals actually reared in zones 2 or 3. Indirect evidence from two independent sources are consistent with this claim. First, males and females resident in zone 1 were found to be depressed in reproductive activity relative to animals resident in zones 2 and 3. Second, very high survival of mice on the grid during the period of study suggested low numbers of dispersers (animals only captured once) were being captured by live trapping (Fairbairn, 1977).

Thus, within the study area, zone 1 appeared to act as a sink or temporary refuge for younger animals. Examination of individual recapture histories revealed that many of these animals survived and relocated to become residents of either zone 2 or 3.

First-captures of adults (n = 156) appeared to be negatively correlated with recaptures within a zone. Fewest first-captures of adults were made in zone 2 (27%) and nearly equal numbers in zone 1 (38%) and zone 3 (35%). First-captures of males and females were not significantly different ($p > 0.05$) among the vegetative zones.

Dispersion, Vegetative Zones, and Population Growth

Changes in dispersion patterns and shifts in habitat occupancy may accompany variations in population density. The unusual increase in density of beach mice observed during this study (see part I of this series and Table 3) provided an opportunity to examine these inter-

actions.

During the period of stable low densities and the period of exponential population growth, there were no differences in average numbers of first-captures among zones (Table 5). However, at peak and declining densities there was a dramatic shift in the pattern of first-captures to favor zone 1 over zones 2 and 3. This was observed even though zones 2 and 3 may be regarded as superior habitat. For example, the density of first-captures in zone 2 at peak population densities dropped to approximately one-half those observed during exponential growth; whereas in zone 1, the first-capture density actually increased between the same two periods. During the time of declining densities first-captures in zone 1 exceeded those in zones 2 and 3.

These results suggest that zone 1 served as a sink for both immature and adult mice during periods of high densities, when zones 2 and 3 were fully occupied by residents. The timing of this occupancy corresponds with the attainment of peak numbers in more optimal habitat and the diminution of breeding activity.

Recapture density was greater in zones 2 and 3 than in zone 1 over all phases of population growth (Table 5). Recapture density was nearest to parity among the zones during peak densities. The dynamics of these changes are revealed by an examination of the ratio of first-captures to recaptures by zone and phase of population growth (Table 5). Residents (i.e., recaptures) predominated in all zones during all phases of population change except in zone 1 during exponential growth. During this period there were actually more first-captures in zone 1 than recaptures. A comparison of the first-capture to recapture ratio

among zones reveals that residents consistently made up a lower proportion of captures in zone 1 than in zones 2 or 3.

In summary, the dispersion patterns of residents and new animals during the different phases of population growth revealed zone 1 to represent suboptimal habitat for beach mice. Zone 2 supported a greater proportion of residents than zone 3.

Residency, Phase of Population Growth, and Vegetative Zones

It can be argued that recaptures within vegetative zones may not represent residents. Establishment of more rigorous standards for classification of residency, i.e., being alive for two or more months, resulted in corroboration of general conclusions reached in the previous sections (Table 6). However, some further subtleties in the dispersion patterns of beach mice were disclosed.

The general notion was confirmed that the rank of habitat quality over a wide range of densities was zone 2 $\geq$ zone 3 > zone 1. However, as shown by Bowers and Smith (1979) with reference to Peromyscus maniculatus in the Great Basin of the western U.S., the sexes did not occupy the habitats (zones) in the same way. The number of resident males in zone 2 was consistently greater than in zone 3. Likewise, the number of males was consistently greater in zone 3 than in zone 1. In contrast, resident females (of breeding status) were consistently more numerous in zone 3, regardless of overall population density. This result is of considerable import and deserves special consideration.

Bowers and Smith (1979) list some selective forces they believe may influence dispersion patterns of P. maniculatus. They suggest the energy costs of reproduction favor segregation of females into the better habitats to satisfy these needs. Also, coupled with the greater food availability in these habitats may be more vegetative cover for concealment from predators. Lastly, habitat partitioning by the sexes may lessen competition between them. I have previously suggested that food plant availability within the zones does not correspond with the local distribution of beach mice. Because beach mice are monogamous, competition between the sexes is not likely to be important. However, the vegetation of zone 3 is the most dense being composed of nearly continuous shrub cover (Table 2). There can be little doubt that the vegetation of zones 2 and 3 is more favorable for protection from predators than that of zone 1.

Movements and Phase of Population Growth

Movements of beach mice as measured by the average distance between captures (ADBC) were relatively modest (< 25 m) for both sexes. Thus, it is realistic to think that many individuals limited the majority of their activities to particular habitat configurations (zones). Contrary to the general pattern among small mammals (Pearson, 1953; Stickel, 1960; Brant, 1962; Shure, 1970), movements of beach mice were not significantly reduced as density changed (Fig. 1). These relationships lead to the conclusion that beach mice tolerate considerable overlap of home ranges and become tightly packed into optimal habitats such as

zones 2 and 3 as density increases.

Habitat Occupancy

Dispersion patterns of beach mice shifted in relation to density changes on my heterogeneous study area. These changes in dispersion patterns appeared to be adaptive and contributed to population increases in marginal habitats. Unfortunately few studies of this type have been conducted with small mammals. To date the most extensive work on the effects of density on habitat occupancy has been done on birds. I will present some of the theoretical considerations resulting from these studies. I do not wish to imply that these models can be wholly applied to small mammals. However, similarities and differences can be discussed and relevance of the concepts to small mammal populations ascertained.

Brown (1969), in a review of territorial behavior and population regulation in birds, described three critical levels of density at which the effects of territorial behavior on dispersion patterns may act. At level 1, densities are low enough that no individuals are prevented from breeding in their preferred habitat. At level 2, however, densities are great enough that some individuals are prevented from settling and breeding in the preferred habitat. These individuals are forced to breed in less productive habitats. At level 3, all habitats are filled where breeding could occur and a surplus of non-breeding "floaters" exists.

Some parallels exist between my observations of beach mouse dispersion and the predictions of Brown's model (1969). I have shown that

based on resident density and reproductive success zone 1 was suboptimal habitat compared to zones 2 and 3. Based on the distribution of new animals and residents among the zones during peak densities, I conclude that density of beach mice was at level 2 as described by Brown. I believe that increased intraspecific interactions, not necessarily territorial behavior, was great enough to cause many individuals to shift into zone 1. I cannot directly demonstrate the existence of level 3 responses from my data. However, Krebs and Myers (1974) suggested that evidence of dispersal onto trapped out areas would be indicative of "floaters" or level 3 conditions in small mammal populations. I have evidence which points to a general lack of dispersal, particularly during the period of high densities. Therefore, I conclude level 3 conditions were probably not present.

Fretwell and Lucas (1969) established as ideal model of habitat selection and distribution. Under the conditions of this model, at low densities animals should be present only in the optimal habitat. Habitat suitability decreases as density increases therefore suitability of the optimal habitat would become lower as density increases, and possibly equal with the suitability of habitats which were less suitable at lower densities. Ideally, at very high densities the suitability of all habitats would be equal. This "ideal" model assumes several conditions, which, as Fretwell and Lucas (1969) noted, do not apply to natural populations. One such assumption is that the success of newly established animals is equal to that of established residents. However, if dominance hierarchies were established, this assumption

would fail. If the density of established residents is high enough, intraspecific interactions may prevent new animals from settling in that habitat. Fretwell and Lucas (1969) described an ideal dominance distribution which takes into account the presence of social dominance hierarchies. It is this distribution which is probably more relevant to the beach mouse population studied, although all phases of the model do not strictly apply. At stable low densities, resident beach mice showed a clear preference for zones 2 and 3. This preference became more obvious during the time of exponential growth, as resident densities increased much faster in zones 2 and 3 than in zone 1. At peak densities two things happened which suggest that intraspecific interactions were high enough in the optimal habitats (zones 2 and 3) to cause zone 1 to be more suitable habitat for new animals: (1) the low number of first-captures in zones 2 and 3 relative to zone 1, and (2) a large increase in resident density in zone 1. The increase in zone 1 resident density between exponential growth and peak densities was five times the resident density increase between stable low densities and exponential growth. This compares with approximately equal increases in zones 2 and 3 resident densities during the time periods described above. Thus, at peak densities zone 1 appeared to become more suitable habitat for new animals to establish residency in than during the periods of stable low densities or exponential growth.

I do not think that the quality of zone 2 or 3 decreased as density increased but rather intrinsic factors (i.e., intraspecific interactions) at high densities caused the suitability of these zones to be lower for new animals and resulted in a shift into zone 1. Grant and Morris

(1971) hypothesized that for animals living in patchy environments, habitat structure (extrinsic factors) was more important than intraspecific interactions (intrinsic factors) in determining dispersion patterns. However, they also hypothesized that increasing density would modify the relationship between habitat structure and dispersion patterns, i.e., one might observe a tendency to go from aggregated toward uniform dispersion patterns as density increases. They cited Bendell (1961) in support of their hypothesis. Bendell (1961) found that Peromyscus leucopus introduced onto an island showed a trend towards uniform dispersion as density increased, in spite of the existence of a patchy environment. My results are also in agreement with the hypothesis of Grant and Morris (1971). At stable low densities and even during exponential population growth, habitat structure appeared to be more important in determining dispersion patterns. However, at high densities this relationship broke down, presumably owing to increased intraspecific interactions; and dispersion approached a more uniform pattern. Vegetative cover appeared to be more important in determining habitat occupancy than food availability. This is in contrast with results of Batzli (1968) for Microtus californicus, but in agreement with what Pitts and Barbour (1979) found for Peromyscus maniculatus in a beach habitat. Apparently cover from predators is more important than food availability in determining dispersion patterns of small mammals living in beach habitats.

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